

# **Perception, cognition, and response: A recognition systems analysis of avian egg rejection**

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## **Abstract**

To claim and understand the uniqueness of any physical, chemical, or biological system, it is necessary to use the same set of approaches, tools, and analyses to probe other systems. Accordingly, to assess whether and how people are unique in their perceptual, cognitive, and behavioural skills and algorithms when making decisions, a parallel set of studies is required to examine how human and non-human animals would respond. This thesis provides a structured experimental analysis of each of the recognition system's components; perception, cognition, and response; in the context of avian brood parasitism. The study species are several potential hosts of brood parasitic birds but an explicit aim of this work to provide a reference for future studies on how to probe the perceptual, cognitive, and response traits in non-verbal experimental paradigms, including non-hosts and working with people.

Hosts of avian brood parasites represent a powerful experimental system in which to study well defined and evolutionarily relevant behavioural decision: brood parasitic birds lay their eggs in other nests and the costs of parental care and reduced reproductive success are borne by the hosts. Hosts, in turn, may reject costly parasitism by ejecting foreign progeny or deserting parasitized nests. The cues used by hosts to perceive, recognize, discriminate, and respond to foreign eggs have been well studied in a variety of avian host-parasite systems. How, in turn, the hosts' sensory and cognitive processes receive, sort through, and determine the behavioural responses to these cues, remains mostly unclear.

The main chapters of the thesis set out to describe the results of two unpublished studies on hosts' recognition systems. The first study uses artificial colour manipulation of hosts' own eggs to determine whether specific colours are perceived similarly to trigger rejection behaviours, irrespective of the presence of hosts' own eggs in the nest. The results suggest that foreign egg colours are perceived similarly and rejection is triggered through comparisons with internal filters, or recognition templates, even when hosts' own eggs are not present. The second study also uses artificial colour manipulation to assess the hosts' specific behaviours to foreign eggs and reveals that relative patterns of egg ejection and nest desertion are indicative of hosts' responses to foreign eggs.

These results provide detailed new information for our understanding of parasitic birds' impacts on hosts' perceptual processes. It is also the aim of this thesis that these studies may also be used as starting points towards a sample set of methodological and analytical tools to determine whether and how other species, including people, may use similar perceptual, cognitive, and behavioural decision rules to detect foreign items in odd-egg-out paradigms.

## Acknowledgements

This thesis is dedicated to all birds, whether native or introduced, living in Aotearoa and Magyarország (Hungary), my two home lands. I am most grateful to Dr Jason Low for taking on the unexpected task of working with me as an adviser, supervisor, colleague, and confidant during the past year. I am very glad for your patience and insights, because this project has been as much a scientific enterprise as a personal exploration of the goals of academic studies and research and an inquiry into whether and how returning to formal schoolwork was for me. For enrolment, approval, support, and reminders, I owe much gratitude to the faculty, administration, and staff of the School of Psychology, Faculty of Science, Victoria University of Wellington. For funding, I thank to the faculty and staff of Hunter College of the City University of New York, for continuing to provide me with a monthly income, and the Human Frontier Science Program, for allocating generous research funding throughout this work. Animal ethics protocols were approved by OTKA in Hungary, University of Auckland AEC in New Zealand, and Hunter College IACUC in the USA. This thesis could not have been completed without the dedicated collaboration and my continued interactions with two research teams: the complex experimental protocols and daily nest checks were part of my collaboration with Miklós Bán, Drs Csaba Moskát, and Zoltán Barta, assisted by others in the field in Hungary. In turn, my work on blackbirds and song thrush were assisted by Peter Samaš, Drs Mike Anderson, Tomas Grim, Jarkko Rutila, Phill Cassey, and by others throughout my field sites in New Zealand. For comments on the examined draft, I thank Drs KC Burns and Dianne Brunton. I am very grateful to P. Samaš for the cover image of a song thrush ejecting an all black egg in New Zealand. To all, a thousand thanks.

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## Background and Overview

Brood parasitic birds deposit their eggs in the nests of other individuals or species, sparing the cost of providing care for their own young (Croston & Hauber, 2010). The result is often a coevolutionary arms race of sophisticated host defences to circumvent or reject parasitism and escalating steps of parasite breaches of host defences (Rothstein & Robinson, 1998; Lyon & Eadie, 2004). Brood parasitism may be obligate, with all eggs are laid in others' nests, or facultative, with some own eggs incubated and others in foreign nests (Davies, 2000). Interspecific brood parasitism involves the laying of eggs in other species' nests, whereas in intraspecific parasitism eggs are laid in nests of conspecifics (Davies, 2000).

Irrespective of the type and mechanism of parasitism, theory predicts that hosts should reduce or eliminate the many costs of parasitism to increase the benefits of parental care for own genetic progeny (Servedio & Hauber, 2006). In turn, some parasites trick hosts by producing perceptually mimetic eggs (Avilés, 2008), laid into a clutch of several of the hosts' own eggs during laying stage (Moskát & Hauber, 2007), with their thicker eggshells making it more difficult or even impossible to puncture and eject (Antonov et al., 2009). The sensory, perceptual, and behavioural responses triggered by parasitic eggs therefore set the stage for testing each of the SENSORY, COGNITIVE, and BEHAVIOURAL limits of the hosts' recognition systems (see Discussion and Implications chapter). This thesis sets out to experimentally address each component of the tripartite recognition systems approach (*sensu* Sherman et al., 1997, Fig. B.1).

# Recognition Systems

**Sherman et al., 1997:**

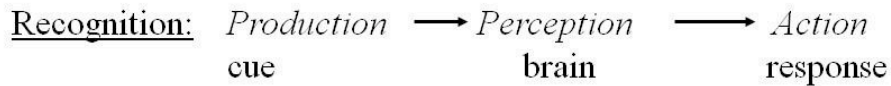


Figure B.1. Schematics of the recognition systems approach, as outlined by Sherman, Reeve, and Pfennig 1997.

The structure of the thesis includes this conceptual introductory chapter, which is my own work, revised following comments on an earlier draft on this and all other chapters from my M.Sc. adviser at the School of Psychology, Victoria University of Wellington, J. Low. This is followed by Chapter 1, which describes a complex set of experiments whose aim was to understand the sensory basis of egg rejection by applying the same set of colour manipulations to a single, several, or all eggs in the clutch of a rejecter host. The central hypothesis of this study was that sensory cues for egg rejection include the perceived difference between own and foreign eggs, irrespective of whether own eggs are available for inspection or need to be remembered. The prediction of this hypothesis was that eggs with the same colour manipulations would be rejected at relatively the same rates, irrespective of the number of eggs treated in the clutch.

The second focus of the experiment was to test the hypothesis that the cognitive basis of egg rejection involved self-referencing through the concurrent inspection of the hosts' own and foreign eggs. This hypothesis was again tested from the data yielded



by the manipulation of different numbers of host eggs with colour treatments, including clutches where all host eggs were dyed. The analytical approach to the data from this study allowed the testing of both of these types of hypotheses in chapter 1.

Specifically, this study's overall premise was that many hosts of avian brood parasites have evolved egg discrimination to reduce the cost of parasitism (Davies, 2000). Great reed warblers (*Acrocephalus arundinaceus*) in Hungary are frequently parasitized by common cuckoos (*Cuculus canorus*), and use several cognitive mechanisms to accurately reject a foreign egg in a clutch of own eggs, even when that egg is closely mimetic (Hauber et al., 2006). Yet, antiparasite defences are less effective when the host clutch is parasitized by multiple cuckoo eggs, suggesting a role for discordancy and/or self-referent phenotype matching of own eggs against foreign eggs (Moskát et al., 2009). The experiments here consisted of three treatments, dying hosts' own eggs with one of several artificial colours so that clutches contained (a) 1 dyed egg and 4 unmanipulated own eggs, (b) 3 differently dyed eggs and 2 own eggs, and (c) 5 differently dyed eggs. Rejection rates of dyed eggs in treatment (a) varied widely for the different colours (7-77%). Critically, however, relative rejection rates of dyed eggs were also consistent between the eggs of the different artificial colours applied, and for some eggs, rejection rates exceeded responses to control eggs. These results support the hypothesis that the sensory basis of egg rejection of own and foreign eggs is the perceived difference between acceptable and unacceptable phenotypes. In support of both a discordancy and self-referencing based cognitive mechanisms to identify and recognize foreign eggs, rejection rates were lower in treatments (b) and (c). These results indicate that in the absence of discordancy or self-referencing, these hosts may rely on comparisons of

foreign eggs against a recognition template. The implication is that simultaneous comparisons of own and foreign eggs are not always required for the perceptual and cognitive processes leading to behavioural rejection of eggs. My contribution to the study was to conceive and design the complex set of experiments to complete the study, to fund and participate in the field work and analyses, and to produce a write-up suitable to be submitted for peer-review in the *Journal of Comparative Psychology*, as corresponding author together with co-authors M. Bán, C. Moskát, and Z. Barta.

Chapter 2, in turn, is based on a study which addresses the behavioural manifestation of egg rejection decisions in response to foreign egg colours in rejecter hosts' nests. Specifically, I designed a set of experiments which utilized the availability of two different rejecter species coexisting in sympatry within the New Zealand landscape, the introduced *Turdus* thrushes of the European blackbird (*T. merula*) and song thrush (*T. philomelos*) (Evans et al., 2005). The study takes advantage of past theoretical work on life history theory predicting that the responses of hosts to reject avian brood parasitism will be shaped by the extent of costs, which in turn is a function of both parasitism rate and the virulence of the parasite (Hauber, 2003). Accordingly, suitable hosts of more virulent nestmate-evictor parasites should eject parasite eggs, irrespective of clutch size, while hosts of less virulent nestmate-tolerant parasites, with smaller clutch sizes, should desert parasitized clutches (Servedio & Hauber, 2006). These contrasting predictions can therefore be used to evaluate the extent of brood parasitism's cost under which egg rejection behaviours in *Turdus* thrushes may have evolved.

For this study, the egg rejection behaviours of European blackbirds, *T. merula*, and song thrush, *T. philomelos*, in their introduced range in New Zealand, were experimentally induced by manipulating the colour of one of the birds' own eggs. The results showed that eggs dyed all black were more often rejected than eggs dyed with 20 black spots but with the background colour left visible. Rejections of all black eggs occurred mainly through nest desertion in blackbirds, which have smaller clutch sizes, and mainly through egg ejection in song thrush, which have larger clutch sizes. The results demonstrate that the use of control manipulations and the detailed assessment of the behavioural outcomes of hosts' responses to experimental manipulations are critical. This is because both, or either, nest desertion and egg rejection can be experimentally induced as the response behaviours of these hosts to the presence of foreign egg colours in their nests. My contribution consisted of the full conception of the study, including the application of published theory to generate novel predictions for these two species regarding their behavioural outcomes in response to experimental parasitism. I conducted the largest block of the field experiments, analyzed all of the resulting data set, and produced drafts of the resulting manuscript and thesis chapter, to be expanded with the addition of a new set of data from a common cuckoo host in Finland, the common redstart (*Phoenicurus phoenicurus*), to increase phylogenetic breadth for comparative analyses. I will submit this manuscript as first author to the comparative psychological journal *Behavioural Processes*, with co-authors P. Samaš, M. Anderson, T. Grim, J. Rutila, P. Cassey, and J. Low.

The final section of the thesis overviews the conceptual, methodological, and experimental benefits of applying the recognition systems approach in studying host-parasite interactions, and will form the basis of a first-authored, invited, peer-refereed

manuscript, co-authored with C. Moskát and J. Low, to be submitted to a special issue of the journal *Avian Biology Reviews*. This section addresses the possibility that the experimental tool sets of avian host-parasite research may be applicable to several other fields of experimental psychology, both in research and in teaching. As such, the aim of this final section is to illustrate a set of experimental scenarios, questions, and predictions to probe animal and human minds, for example through class-room applicable, hands-on, computer-screen based experiments. These experiments may then be used to illustrate both the cognitive conclusions and the powerful hypothesis-testing implications that can be drawn from concurrently designed and parallel-run experimental designs, providing a novel relevance of avian host-parasite research for studies of general, non-host including human, dimensions of animal cognitive complexity.

## **Chapter 1:**

### **Testing alternative perceptual and cognitive mechanisms to reject brood parasitism in the presence and absence of hosts' own eggs**

Obligate avian brood parasites lay their eggs into the nests of other bird species (Davies, 2000), relying on hosts to incubate foreign eggs and to provision parasitic nestlings (Payne, 2005). The benefits and the costs of brood parasitism to elicit parental care for genetically unrelated young represent an important evolutionary selection pressure, so that, respectively, typical avian brood parasites show morphological and behavioural adaptations to exploit hosts, and these hosts often show antiparasite adaptations to reduce the costs of parasitism (Dawkins & Krebs, 1979; Krüger, 2007; Rothstein & Robinson, 1998).

In the co-evolutionary arms race between parasite and host sometimes hosts win, and eliminate the parasites altogether (Lovász & Moskát, 2004). Alternatively, brood parasites may have only recently begun to parasitize some host species so that these have not yet evolved antiparasite responses (Hauber et al., 2004), or parasitic mimicry is so perfect that the hosts' sensory systems cannot detect foreign eggs or young in the nest (Avilés, 2008; Ranjard et al., 2010). In most cases studied, however, the arms race is ongoing, and some parasitism attempts succeed against the imperfect defence repertoire of hosts' antiparasite responses (e.g. Davies & Brooke, 1988; Moksnes et al., 1993, Moskát & Honza, 2002; Takasu et al., 2009). If some of the hosts possess the ability to recognize and reject the parasite egg(s), this may stabilize both the population level interactions of the hosts and brood parasites (Barabás et al., 2004; Takasu et al., 1993). Accordingly, foreign egg discrimination is typically the most

important antiparasite adaptation for many host lineages, although the arms race may escalate to include chick discrimination and the evolution of host-parasite chick mimicry (Grim, 2006; Langmore et al., 2003, 2011; Schuetz, 2005).

The most extensively studied avian brood parasite is the common cuckoo (hereafter: cuckoo), whose females form host-specialized races (*'gentes'*), showing egg mimicry of a particular host species; in turn, most hosts of the cuckoo show behavioural strategies to discriminate and reject imperfect mimic foreign eggs (e.g. Davies & Brooke, 1988; Hauber et al., 2006; Moksnes et al., 1991; Røskft et al., 2002). Cuckoo eggs typically resemble host eggs in colour and pattern (Davies & Brooke 1988, 1989; Moksnes & Røskft, 1995), but not in egg shape (Bán et al., 2011), to generate a sensory image that closely mimics the hosts' own eggs' appearance (Avilés, 2008; Cassey et al., 2008a). The cognitive basis of behavioural responses to brood parasitism has been considered to include both self-referenced and socially learned signals of the parasitic eggs', chicks', and adults' phenotypes (Lotem et al., 2005, Moskát & Hauber, 2007). For example, the discrimination of own versus foreign eggs appears to depend on how the avian sensory system receives visual information (Avilés, 2008; Cassey et al., 2008a; Spottiswoode & Stevens, 2010; Stoddard & Stevens, 2010, 2011) and interprets the differences between the physical patterns of coloration and maculation of own versus foreign eggshells (Cherry et al., 2007; Davies & Brooke, 1989; Honza et al., 2007; Moskát et al., 2008b; Røskft & Moksnes, 1991).

The behavioural process of egg discrimination can be divided into several main parts, as defined by recognition systems analyses (Sherman et al., 1997): the perception of

the eggshell, the cognitive algorithms involved in recognizing and generating a response to perceived cues, and the behavioural responses (if any) to the egg, including the cases when hosts recognize the foreign eggs but are unable to pierce or grasp, or decide not to reject them (Antonov et al., 2009; Davies et al., 1996; Hauber & Sherman, 2001; Moskát & Hauber, 2007; Spottiswoode, 2010). Most studies to date have used data on the subjects' displays of behavioural patterns and outcomes of egg rejection to infer perceptual abilities of egg discrimination (Avilés, 2008; Cassey et al., 2008a; Spottiswoode & Stevens, 2010; Stoddard & Stevens, 2010, 2011), while others used video-observations on duration of inspection, latency to reject, and patterns of egg-pecking to reveal that discrimination can take place before or in the absence of egg rejection (Antonov et al., 2009; Honza et al., 2007; Soler et al., 2002). To integrate perceptual and behavioural processes to identify the perceptual and cognitive basis of egg discrimination cues and thresholds requires in depth data collection using a combination of artificial parasitism and dynamic experimental manipulation of host egg appearance in space and time (Hauber et al., 2006).

Another approach of testing alternative cognitive mechanisms underlying egg discrimination by potential hosts is to apply a standard experimental design to a large sample of host nests and to concurrently test alternative cognitive decision rules contributing to egg rejection (Hauber & Sherman, 2001; Moskát & Hauber, 2007). For example, Moskát et al. (2010) demonstrated that a regular host of the cuckoo, the great reed warbler (*Acrocephalus arundinaceus*), relied on both of two different cognitive methods of egg recognition. One of these mechanisms was discordancy, where hosts reject the egg phenotype in the minority, while accept the egg phenotypes in the majority in the clutch (Rothstein, 1974). Accordingly, in the great reed warbler,

10% of these hosts ejected even their own eggs ( $n = 30$ ), when clutches contained four parasitic eggs and one own egg (Moskát et al., 2010). The alternative, but not mutually exclusive, mechanism was template recognition, whereby birds compared each egg against an internal, recognition template of own eggs, probably learned shortly after laying (Moskát & Hauber, 2007). The experimental separation of the two decision mechanisms required specially designed treatments of several different manipulations of dying a single egg, dying all but one egg in the nest, and dying all eggs in the nest, conducted concurrently in different host clutches, to test alternative cognitive mechanisms of foreign egg recognition (Moskát et al., 2010). The results revealed the simultaneous use of multiple cognitive algorithms by these hosts in rejecting foreign eggs. This finding was consistent with the hypothesis that multiple decision rules working in parallel may be beneficial in reducing recognition errors through redundancy (Hauber et al., 2000), including cuckoo egg rejection in those host populations, where parasitism rates are high, egg mimicry is good, and clutches are exposed to instances of multiple parasitism (Moskát et al., 2009).

Critically, neither discordancy based on clutch learning (Hauber et al., 2004; Hoover et al., 2006; Rothstein, 1974, 1975), nor recognition templates (Moskát & Hauber, 2007; Lotem, 1993; Lotem et al., 1995) need to involve the concurrent inspection and comparison of own and foreign eggs at the same time in the nest (*sensu*: online self-referenced comparison, Hauber & Sherman, 2001). In turn, when faced with high and multiple parasitism rates, where cuckoos replace host eggs with parasitic eggs, hosts' own eggs may frequently be in the minority or altogether absent in host nests during the laying or during the incubation period (Hoover, 2003; Rothstein, 1974; Trine, 2000). As such, hosts faced with high parasitism rates are predicted to recognise



foreign eggs in the absence of own eggs in the clutch. Cuckoos parasitize great reed warblers in Hungary at unusually high rates, causing more than 50% parasitism rate in habitats where trees are available for vantage points for cuckoos (Moskát et al., 2008a; Røskoft et al., 2002;). A consequence of heavy cuckoo parasitism, timed closely during the hosts' laying cycle (Moskát et al., 2006), is the high frequency of multiple parasitism. However, previous work on great reed warblers in Hungary, also revealed that the reduced numerical and proportional presence of hosts' own eggs in a naturally or experimentally parasitized clutch is predictive of lower cuckoo egg rejection rates in great reed warbler nests, including in natural clutches with multiple parasitism (Moskát et al., 2009) and in experimental clutches with multiple variably-mimetic dyed eggs (Moskát et al., 2008b). Similarly, rates of rejections of natural cuckoo eggs decrease with more host eggs in the nest or when own eggs are experimentally exchanged with foreign eggs during the hosts' laying period (Moskát & Hauber, 2007). Critically, in all these cases, the relative numbers of own vs. foreign eggs were variable, thus implying a potential role for the *in situ* simultaneous, online comparison of own and foreign eggs in the nests (Hauber & Sherman, 2001).

Here a unified set of parallel experimental manipulations was again used, this time to specifically test the first two components of a recognition systems based approach to the study of avian brood parasitism and egg rejection displays. The aim was to test the hypothesis whether perceptual consistency exists regarding the sensory inputs of foreign egg coloration relative to acceptable-to-unacceptable egg phenotypes. Previous work showed that the decision to accept or to reject inaccurate (moderately) mimetic foreign eggs was based on contextual cues: the same egg phenotype (20 spot egg) which was overwhelmingly accepted by hosts was in turn overwhelmingly

rejected following the introduction of a highly non-mimetic foreign egg (Hauber et al., 2006). However, in this previous work only a single type of moderately mimetic egg manipulation was used, which did not allow the examination of whether and how differently mimetic egg types would elicit the same relative extent of egg rejection decisions, irrespective of contextual cues (i.e. the presence of other foreign eggs). Such an experiment was carried out here by repeatedly utilizing the same set of egg colour manipulations of hosts' own eggs in clutches with a single, several, and all own eggs experimentally dyed. The prediction of the perceptual constancy hypothesis was that irrespective of the absolute levels, the relative rates of egg rejection should remain consistent across the different treatments and clutch content manipulations.

In turn, regarding the cognitive basis of egg rejection decisions, the goal was to set out to examine the role and relevance of self-referencing and other cognitive mechanisms underlying egg rejection decisions by cuckoo hosts. The experimental approach was to specifically examine the role that the presence of own eggs might play in facilitating egg discrimination by great reed warbler hosts of the common cuckoo, while simultaneously manipulating the feasibility of both discordancy- and recognition template-based cognitive rules to contribute to egg rejection decisions. It was hypothesized that hosts' egg rejection ability would be reduced in a range of experimental multiple parasitism, especially in cases where all eggs were treated to be parasitic, in contrast with experimental single parasitism. Accordingly, the prediction was that hosts would reject fewer eggs in multiple than in single parasitism. A second, novel hypothesis was also tested that the presence of hosts' own eggs, within a mixed clutch of own and foreign eggs, would increase hosts' egg recognition rates through self-referencing; it was predicted that great reed warblers would reject more foreign

eggs in multiple parasitism when hosts eggs are also present relative to clutches where all of the hosts' own eggs are experimentally replaced with foreign eggs. Third, to integrate these hypotheses, a range of artificial colours was used to dye hosts' own eggs to determine whether colour-dependent egg rejection rates in great reed warblers covaried with the presence, and thus potentially involve the inspection, of own eggs. It was predicted that in the absence of self-referencing own eggs, colour-dependent egg rejection rates would also decline.

## **Methods**

The study was conducted in the surroundings of Apaj (47°07'N; 19°06'E), ca. 40-60 km south of Budapest, Hungary, during the northern spring and summer of 2009 and 2010, from mid-May until mid-June. Great reed warblers breed in 2-4 m wide reed-belts along both sides of narrow irrigation channels. Sections of the channels were monitored every week to find nests during the nest-building or egg-laying stages. One or more host eggs in a clutch were manipulated using highlighter pens (type Stabilo Boss), of blue, green, yellow, orange and red highlighter colours (No. 70/31, 70/33, 70/24, 70/54, and 70/40, respectively), to dye the hosts' eggs (Figs 1.1 & 1.2). Representative spectrophometric reflectances (Cassey et al., 2008a) of the differently dyed eggs are illustrated in Fig. 1.1. In our own prior work, background colour manipulations with these and other colours have caused vastly different rejection rates (Hauber et al., 2006; Moskát et al., 2009).

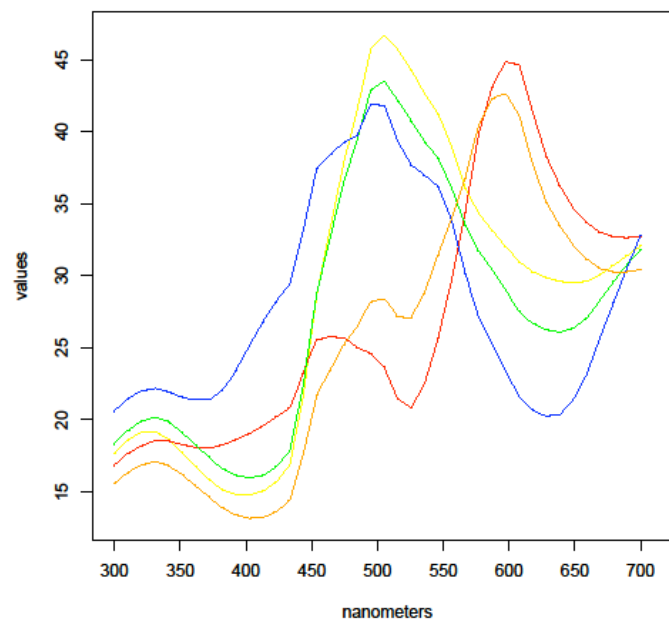


Figure 1.1. Representative clutch (above) and relative % reflectance curves (below, y-axis against wavelength on x-axis) of the background colours of great reed warbler eggs dyed with one of five different colours (blue, green, yellow, red and orange). Photo credit: Mark E. Hauber.

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This approach was demonstrated to be suitable for studying experimental parasitism in great reed warblers, because even though cuckoo eggs are thicker and stronger than host eggs, this host is able to reject cuckoo eggs by puncture ejection and parasite and host eggs are comparable in size (Antonov et al., 2008; Hargitai et al., 2010) and highlighter dyed eggs had been found to be ejected by this host in previous studies (Moskát et al., 2010). The following treatments were applied to nests in the study (Fig. 1.2.):

(a) Treatment ‘1-egg’: One host egg per clutch was manipulated, using one of five colour types at a time, with one of the five highlighter pen colours at a clutch, so the original maculation pattern also remained visible. Experiments were started in the second half of the laying stage (3-5 eggs/nest).

(b) Treatment ‘3-eggs’: Three eggs were manipulated in a clutch with different colours, using the blue, yellow and orange pens. In preliminary trials which included several cases from Treatment (a) above, these three colours were recorded to evoke the lowest, intermediate, and highest values of rejection frequency. Experimental manipulations were done by dying 3 eggs simultaneously when clutches were completed with five eggs, assuring that the majority of eggs in the nest were dyed.

(c) Treatment ‘5-eggs’: All eggs in five-egg clutches were dyed using different colours from Treatment (a) simultaneously in each clutch. Experiments were started on the day when hosts laid their fifth egg.

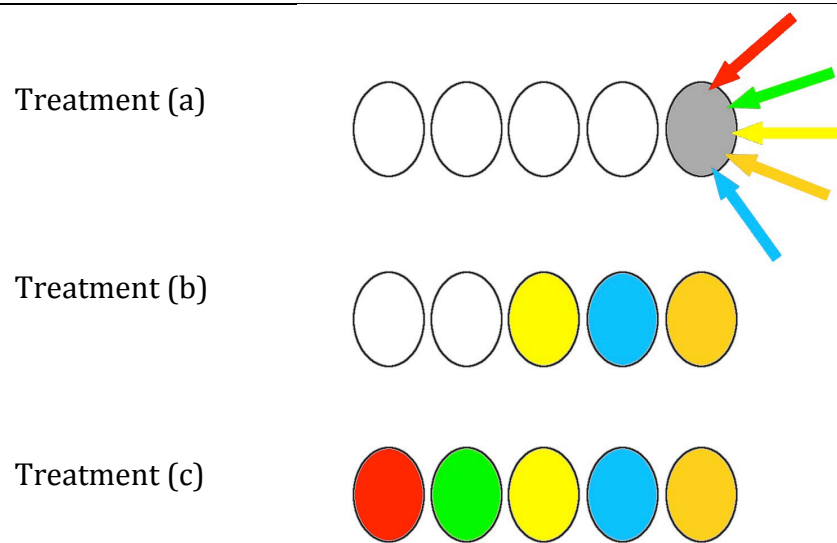


Figure 1.2. The experimental schematics of three treatment types for testing egg ejection in single parasitism (a) and multiple parasitism, either when two natural coloured eggs (white) of the host are present (b) or when none are present in the clutch (c). Five colours were applied for treatments (a; 12-17) and (c; 17): blue (14), green (15), yellow (12), red (16), and orange (13), and three colours were used for treatment (b; 16): blue, yellow and orange (illustrated below prior and after dyeing; the bottom right brown egg illustrates the egg type used previously in Hauber et al., 2006). Sample sizes (  $n$  = nests) are indicated in brackets. Photo credit: C. Moskát.

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Experimental nests were checked until 6 days after the treatment on a daily basis to determine host responses. A clutch was deemed deserted during the daily check period when there were cold eggs and then no rotation of the eggs was observed between subsequent visits. If hosts ejected one or more eggs from clutch, the result was classified as ejection. If the manipulated eggs remained in the clutch at the end of the check period (6 days), the result was considered as acceptance (Hauber et al., 2006; Moksnes et al., 1991; Moskát et al., 2010.)

Individual hosts were not colour banded in this study but studied nests that were sufficiently distant and synchronous within years to reduce pseudoreplication; between years this host species shows a low level of breeding philopatry in this study population (Moskát et al., 2008a). Accordingly, each nest was considered as the unit of statistical analysis, with minimal chances of pseudoreplication at the level of host territory and breeding pair. Linear models were applied for the analyses of host rejections toward the parasitic eggs in the different treatments. For testing hosts' reactions toward the differently coloured eggs in single parasitism (Treatment [a]), applied nominal logistic regression was run, which included host responses to parasitism (eject/accept) as a binary response variable, with laying date as a covariate and treatments as factors. From rejections either by ejection or desertion, only ejections were considered, because almost all of the responses belonged to this category, and only one case of desertion was observed, in Treatment (a), in response to a green dyed egg.

The two treatments of multiple parasitism (Treatments b and c) were compared using a generalized linear model, where the response variable was the percent of parasitic

eggs ejected (square-root transformed), with laying date as covariate, and Treatments as nominal factors, in SPSS ver. 17.0. As above, host responses included ejections and acceptances, only. Generalized linear mixed effect models (Bates & Maechler, 2009) were also used to estimate the effect of individual colours and treatments on the acceptance rates of an egg. The models have been fitted using the Laplace approximation criterion. Two-tailed tests were used with  $\alpha = 0.05$ .

## **Results**

In Treatment (*a*), when only one egg was dyed in the clutch, rejection rates toward the five different colours increased in the following order: blue < green < red < yellow < orange (Fig. 1.3).



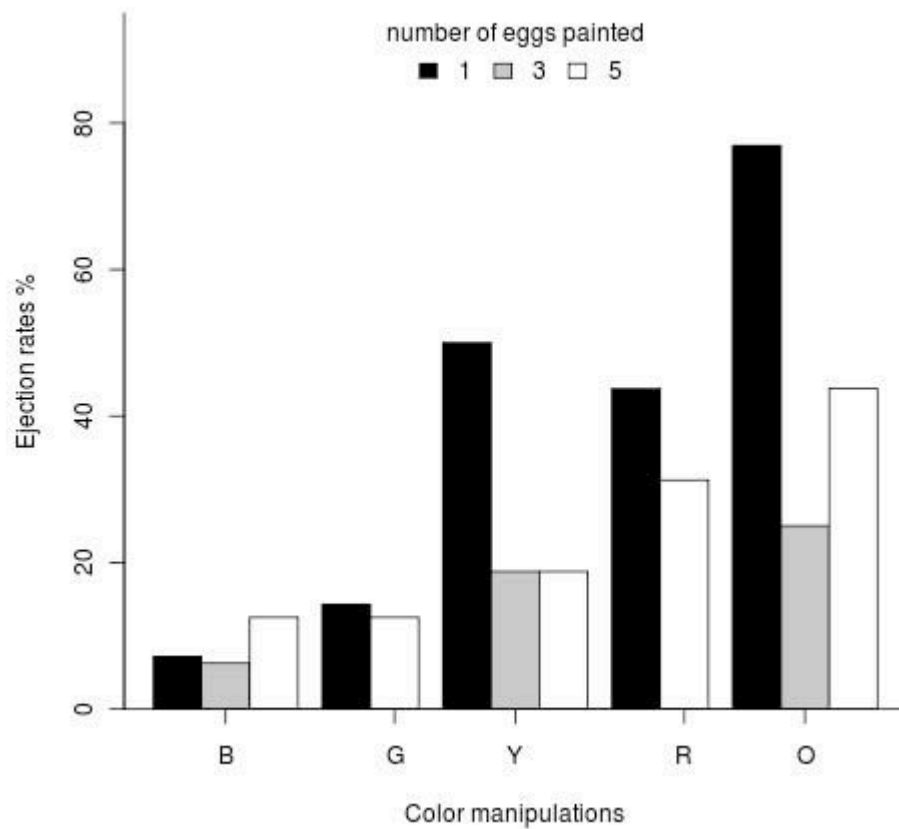


Figure 1.3. The proportion of nests where at least one painted egg was ejected by hosts in response to experimental parasitism with dyed own eggs. Note that number of colours was five in treatments (a: 1-egg) and (c: 5-eggs), with only one colour used at a time in (a), while three colours (blue: B, yellow: Y, and orange: O) were used concurrently in treatment b: 3-eggs, and did not include green (G) and red (R).

Nominal logistic regression revealed that both laying date and colour significantly affected egg ejection rates of hosts. Responses to green eggs did not vary from those to the other egg colours, but responses to yellow, red and orange eggs differed from responses to blue eggs (Table 1.1). Acceptance rates of the same egg phenotypes in Treatment (c), showed a consistent pattern relative to acceptance rates detected in Treatments (a) and (b) (restricted to blue, yellow, and orange dyed eggs, of the colours present in all three treatments, Fig. 1.3; Friedman test:  $\chi^2 = 6.00$ ,  $P = 0.0498$ ).

Table 1.1. Parameter estimates for host responses to dyed egg(s) in experimental parasitism with one parasitic egg per clutch. Five differently coloured host eggs were used as parasitic eggs: blue, green, yellow, red and orange ejections were compared to blue colouring. Only egg ejections were considered.

Parameter Estimates						
	Std.					
ejections <sup>1</sup>	B	Error	Wald $\chi^2$	df	Sig. (P)	Exp(B)
Intercept	-0.583	1.202	0.235	1	0.628	
laying	-0.207	0.074	7.939	1	0.005	0.813
green	0.791	1.341	0.348	1	0.556	2.205
yellow	2.590	1.246	4.319	1	0.038	13.331
red	2.669	1.225	4.748	1	0.029	14.430
orange	4.071	1.336	9.287	1	0.002	58.608

<sup>1</sup>reference category: acceptance of blue egg

Hosts' reactions in the two treatments of multiple parasitism (Treatments *b* and *c*) proved to be statistically similar when ejections per nest were considered on a binary basis (yes/no), but in Treatment *c* host ejected proportionally more dyed eggs than in Treatment *b* (Generalized Linear Model: treatment: Wald  $\chi^2 = 4.260$ ,  $df = 1$ ,  $P = 0.039$ , laying date: Wald  $\chi^2 = 0.152$ ,  $df = 1$ ,  $P = 0.696$ , category \* laying: Wald  $\chi^2 = 2.743$ ,  $df = 1$ ,  $P = 0.098$ ). Parameter estimates were significant for the Treatment effect, only ( $B = 10.135$ , S.E. = 4.911, Wald  $\chi^2 = 4.260$ ,  $df = 1$ ,  $P = 0.039$ ).

The probability of ejection of differently dyed eggs was also quantified as the transformed estimates of the fitted model (Table 2). The orange eggs had a higher probability to be rejected than yellow eggs which in turn had higher probability of rejection than the blue eggs across all treatments. When there were 3 dyed eggs (Treatment *b*), the probability of rejection was less than when there was only one dyed egg (Treatment *a*). When there were 5 dyed eggs (Treatment *b*), the probability of rejection was not significantly different than when there were single dyed eggs (Treatment *a*) (Table 1.2).

---

Table 1.2. Estimates of rejection rates for the different colours and treatments.

Generalized linear mixed models were fit by the Laplace approximation: Formula:

ejections  $\sim (1 | id) + colour + dyed\ eggs$ .

	GLMM logistic parameter estimates	Std. Error	z	P
Blue	-2.542	0.790	-3.220	0.001*
Green	0.165	1.039	0.159	0.874
Yellow	1.983	0.858	2.312	0.021
Red	2.272	0.889	2.555	0.011
Orange	3.447	0.854	4.036	<0.001
Painted 3 eggs	-2.430	0.906	-2.684	0.007
Painted 5 eggs	-1.217	0.743	-1.638	0.101

## Discussion

Regarding the sensory basis of egg rejection in great reed warblers, these experiments provide support for a relative perceptual order of acceptable-to-unacceptable artificial egg colours, irrespective of the presence or relative number of hosts' own eggs in the clutch. Specifically, the comparison of the three artificial egg colours used in all three experimental treatments confirmed that blue eggs are accepted the most, relative to yellow, and orange eggs are accepted the least often by this host species (Fig. 1.3. and

the respective Friedman test's output). The statistically consistent relative order of the hosts' behavioural responses to these egg colours, even when additional colours (green and red) were included in the clutch and even when no own eggs were available for inspection, is in support of the perceptual consistency hypothesis.

Regarding the cognitive basis of egg rejection decisions, great reed warblers are likely to use multiple cognitive rules to discriminate own and foreign eggs, as was previously demonstrated (Moskát et al., 2010). Here, strongest rejection responses against the experimentally dyed eggs were recorded when host nests contained one (Treatment *a*) over three or five experimental, 'parasitic' eggs (Treatments *b* and *c*). These results confirm the hypothesis that hosts' egg rejection responses are reduced in multiple parasitism with increasingly more variable egg phenotypes (Moskát et al., 2008b). Nonetheless, in Treatment (*c*) when all the eggs were parasitic, hosts could no longer use online comparison of own and foreign eggs, either through self-referencing own eggs or through discordancy based decisions between the relative numbers of own and foreign eggs. In these contexts, then, the conclusion is that host used an internal recognition template to decide whether to eject or not an egg. Whether this internal template was formed at the time of laying each egg (but before we manipulated its appearance) or during earlier nesting attempts (Hauber et al., 2004; Petrie et al., 2009), remains to be tested empirically.

Nevertheless, hosts rejected the fewest proportion of eggs overall, and did not reject all the eggs in Treatment *c*, but in the case of orange eggs, they did so more often than when some natural own eggs were in the nest (Treatment *b*). One explanation is that in the three parasitic eggs and two own eggs case (Treatment *b*), along with the

recognition template-based discrimination mechanism, a special discordancy-based mechanism also acts: discordancy means that hosts reject the egg phenotype in the minority in a clutch. When there is only one parasitic (or dyed) egg in a 5-egg clutch, this is a clear case (Treatment *a*). Similarly, when all the eggs are parasitic except one, which is an own egg, some of the great reed warblers ejected their own eggs (Moskát et al., 2010). In some of the experiments described here (Treatment *b*), the parasitic eggs are still in the majority of the clutch (3 eggs; 60%), but the frequency of own eggs appeared to be also relevant (2 out of 5 eggs; 40%), which may reduce the accuracy of the discordancy effect relative to own eggs. This would result in lower rejection rates in multiple parasitism, which explains the prior discovery of a higher tolerance against cuckoo eggs in multiple than in single cuckoo parasitism (Moskát et al., 2009).

In contrast to great reed warbler hosts, in the brambling (*Fringilla montifringilla*) and chaffinch (*F. coelebs*) a separate study revealed similar rejection rates in single and multiple parasitism with two parasitic eggs (Vikan et al., 2009). These two species can be regarded as abandoned hosts by the cuckoo, and hence the winners of the evolutionary arms race with the parasite, probably because they possess highly-evolved and fine-tuned visual perception and, hence, egg discrimination abilities (Vikan et al., 2009). In the absence of ongoing brood parasitism, it is also likely that bramblings and chaffinches detect parasitic eggs by template recognition only, and do not rely on discordancy based discrimination, as do great reed warblers (Moskát et al. 2010). In support of these alternative evolutionary histories, theoretical models confirm that hosts which tolerate more cuckoo eggs in multiple than in single

parasitism, may have had longer coevolutionary interactions through more stable host-brood parasite population dynamics (Takasu & Moskát, 2011).

When there were more parasitic than hosts' own eggs in the nest, the predicted outcome of discordancy per se was to reject the hosts' own eggs, and that of the template-recognition mechanism is to reject the foreign egg. The reason is that the outcome of these alternative or complimentary mechanisms may be the cancellation of discrimination decisions or the rejection of all eggs in the nest, perhaps through nest desertion. In the experiments here, however, regardless of whether nests were singly or multiply parasitized, hosts rejected the parasitic eggs almost only by ejection (see Results; also see Chapter 2).

Svenningsen and Holen (2010) analyzed the importance of external cues, like the sight of the brood parasite at the nest, indicating brood parasitism for hosts and suggested a scenario in which a repertoire consisting of a variety of host responses, evolved as a consequence of individual differences in hosts' egg discrimination ability, parasite egg mimicry, and external cues, is maintained. Pozgayová et al. (2009) demonstrated sex difference in antiparasite defence in the great reed warbler: males guard nests from intruders, while females check clutches through closer nest inspection. However, females also may have information about the laying attempt of the cuckoo, as in many cases they help the males to attack the parasitic intruder (Davies, 2000). The relative clutch completion state at the time of parasitism during the egg-laying stage of the breeding cycle also has an importance, because hosts tend to desert their clutches when parasitism occurred during the earlier phase of egg laying, when the number of eggs in the clutch is low (Moskát & Hauber, 2007;

Moskát et al., 2011). These experiments were carried out near or upon the completion of the full clutches, and probably this explains the lack of desertion responses detected here following experimental parasitism (again, see Chapter 2).

Overall, the relative proportions of differently dyed eggs rejected in each treatment showed a consistent pattern across all three Treatments, with blue eggs consistently accepted and orange eggs consistently rejected the most often. This finding is in support of a consistent role, or perceptual constancy, of hosts' sensory inputs about the identity of foreign versus own eggs. Regarding the cognitive mechanisms involved in egg rejection decisions, great reed warblers' ejection rates of dyed eggs decreased with increasing proportions of experimental eggs per clutch, from the highest rates in Treatment (a) to lower rates in Treatments (b) and then (c). Given that both the presence/absence and also the relative numbers of great reed warblers' own eggs over dyed eggs varied globally across these experiments, these results are most consistent with an internal, recognition based rejection mechanism operating in these hosts in response to particular colours of foreign eggs.



## **Chapter 2:**

### **Life-history theory predicts alternative rejection responses to foreign eggs of introduced *Turdus* thrushes in New Zealand**

Avian brood parasites vary in the extent to which they reduce the reproductive success of hosts (Hauber, 2003). For example, obligately interspecific *Cuculus* cuckoos and other virulent parasite chicks typically eliminate all of the host's breeding success by evicting nestmates soon after hatching (Hauber & Moskát, 2008). In contrast, less virulent *Molothrus* cowbirds and intraspecific brood parasite chicks, often tolerate host nestmates to grow up together (Kilner et al., 2004). As an evolutionary response, to reduce or to eliminate the costs of avian brood parasitism, hosts may reject parasitism by ejecting foreign eggs and chicks from nests and/or by abandoning (deserting) parasitized broods and initiate a new breeding attempt (Davies, 2000; Hauber, 2003; Hosoi & Rothstein, 2000; Rutila et al., 2006).

From a recognition systems perspective, experimental research on egg rejection in hosts of brood parasites requires the assessment of the hosts' behavioural responses as either egg ejection or nest desertion, or the relative frequencies of these displays. This is necessary to identify whether egg ejection and/or nest desertion is the evolutionarily evolved adaptation of hosts in response to coevolutionary histories with brood parasitism (Moskát et al., 2011). Alternatively, ejection/desertion may be a generalized response to cease costly investment into reduced clutch and brood sizes following partial clutch predation-like egg removal by female brood parasites and

hosts (Kosciuch et al., 2006), or they represent an experimental artefact following the disturbance of manipulating host egg content by researchers (Ruttila et al., 2006).

Furthermore, it remains to be addressed empirically what proximate and ultimate factors determine which mechanisms of rejection behaviours hosts display? Egg ejection, for example, eliminates the immediate the costs of incubating and hatching genetically unrelated eggs, providing parental care for parasitic nestlings, and experiencing loss of fitness due to competition of own chicks with the parasite or the elimination of reproductive success altogether as the parasitic chick evicts all host eggs and nestmates (Grim et al. 2009; Hauber & Moskat, 2008; Kilner et al., 2004). Still, egg ejection is not necessarily cost free for the potential foster parents, as it does not emancipate the host from its nest already having been discovered by the parasite, from the parasitic female typically removing a host egg when laying her own egg, or the return of the parasite to lay additional eggs in the clutch (Hauber et al., 2006; Moskat et al. 2009). In contrast, nest desertion and renesting elsewhere frees the host from providing costly incubation and provisioning to unrelated progeny, but renesting also incurs the costs of locating new nest sites, the time and energy required to build a new nest, and the resources required to laying a new clutch (Servedio & Hauber, 2006). Accordingly, previous theoretical work, based on the extent of phenotypic similarity between host and parasite eggs, the cost of host reproductive investment per breeding bout, the fitness reduction in relative breeding success owing to parasitism, and the rate of parasitism, predicted that hosts may evolve consistently different mechanisms and displays of rejection behaviours to reduce the cost of caring for foreign eggs following in response to brood parasitism (Davies et al., 1996; Reeve, 1989; Servedio & Lande, 2003; Takasu et al., 1993). The critical factor in these

models was the absolute and relative clutch size of egg ejector versus nest deserter host species: in response to moderately costly (less virulent) parasitism, species with larger clutch sizes were predicted to eject eggs and species with smaller clutch sizes were predicted to abandon nests, whereas in response to severely costly parasitism, all species are predicted to respond with egg ejection (Servedio & Hauber, 2006). Comparative data are largely consistent with these predictions of egg rejection methods (of egg ejection/nest desertion) across hosts of several avian brood parasitic lineages (Hauber, 2003; Hosoi & Rothstein, 2000; Langmore et al., 2005; Servedio & Hauber, 2006). The central aim of this study is to provide a critical empirical test of this theoretical model, as applied to two sympatric species of egg rejecter thrush species in New Zealand. The predictions of the model, as applied to these species are summarized in Table 2.1.

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Table 2.1. Predictions of predominant rejection behaviour methods by *Turdus spp.* from life history theory modelling (Servedio & Hauber, 2006).

<b>Virulence (cost of parasitism)</b>	<b>Clutch size: <u>lower</u> blackbird</b>	<b>Clutch size: <u>higher</u> song thrush</b>
<b>Lower</b>	<i>Desert nest</i>	<i>Eject egg</i>
<b>Higher</b>	<i>Eject egg</i>	<i>Eject egg</i>

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Throughout the global distribution of the thrush genus *Turdus*, individual species have been reported to be variably impacted by brood parasites, including both highly virulent, nestmate evictor interspecific parasites (Grim et al., 2011; Honza et al., 2005) and less virulent nestmate-tolerant inter- (Friedman, 1929; Lichtenstein, 1998) or intraspecific parasites (Grim and Honza, 2001; Moskát et al., 2003). Specifically, previous work on European blackbirds (*T. merula*) and song thrush (*T. philomelos*) documented variation in rejection rates in response to foreign (natural or experimental) eggs of heterospecifics or conspecifics, when studied in the context of evaluating the evolved responses of these species to virulent brood parasitism by the common cuckoo *Cuculus canorus* (Hale & Briskie, 2007; Honza et al., 2007). Accordingly, within their European range, in a specific comparison of rural versus urban blackbirds, this species was reported to have rejected non-mimetic (cuckoo-like) eggs at higher rates in rural areas where they bred in sympatry with the cuckoo, compared to nearby urban areas where blackbirds bred in allopatry from the cuckoo (Moskát et al., 2003). These covarying differences in rejection rates between areas of sympatry versus allopatry with the cuckoo imply an evolutionary history and selection pressure on blackbirds to recognize and reject interspecific brood parasitism. In contrast to these conclusions, other reports of blackbirds and song thrush in areas of both in sympatry with the cuckoo, including Britain (Davies & Brooke, 1989a,b), the Czech Republic (Grim & Honza, 2001), and Hungary (Moskát et al., 2003), and also in allopatry in New Zealand (breeding stock introduced from Britain; Hale & Briskie, 2007), recorded consistently high rejection rates of non-mimetic, model cuckoo eggs. These latter reports on the lack of covariation in rejection rates between areas of sympatry or allopatry, in turn, support an evolutionary scenario whereby egg rejection

in blackbirds has evolved in a context other than interspecific brood parasitism (Grim et al., 2011).

With respect to highly mimetic (natural conspecific or artificially painted) eggs, rejection rates of experimental intraspecific brood parasitism by blackbirds and song thrush were low in Europe (Davies & Brooke, 1989; Honza et al., 2007; Moskát et al., 2003) but high in New Zealand (Hale & Briskie, 2007). However, natural parasitism on various *Turdus* species in Europe by common cuckoos is extremely rare (Møller, 1976), these thrushes are generally unsuitable cuckoo hosts, as the parasitic chicks survive poorly in their nests (Grim et al., 2011), and intraspecific brood parasitism has been reported repeatedly for both blackbirds (Moskát et al., 2003) and song thrush (Grim & Honza, 2001) within their European range (Grim et al., 2011). Thus, another possible interpretation of these combined findings from the literature is that egg rejection behaviours blackbirds and song thrush are owing to an evolutionary selection pressure from intraspecific, rather than interspecific, brood parasitism on these species (Grim et al., 2011).

Critically, for the purposes of this study, both nest desertion and egg ejection are part of the behavioural repertoires of these species in response to experimental parasitism (Grim & Honza 2001; Moskát et al., 2003). Within the context of life history theory, interspecific brood parasitism by common cuckoos in general represents a high cost, high virulence trait, because cuckoo chicks evict host eggs and nestmates (Hauber, 2003). In contrast, intraspecific brood parasitism represents a low cost, low virulence trait because host and foreign chicks grow up together in parasitized broods (Kilner et

al. 2004; Servedio & Hauber, 2006). Specifically, modelling work, using egg recognition mechanisms based on host-parasite egg phenotype discrimination, predicted that hosts of more virulent parasites would reject parasitism by the method of ejecting foreign eggs from clutches, while hosts of less virulent parasites with smaller clutch sizes would desert (or abandon) parasitized clutches (Servedio & Hauber, 2006) (Table 2.1).

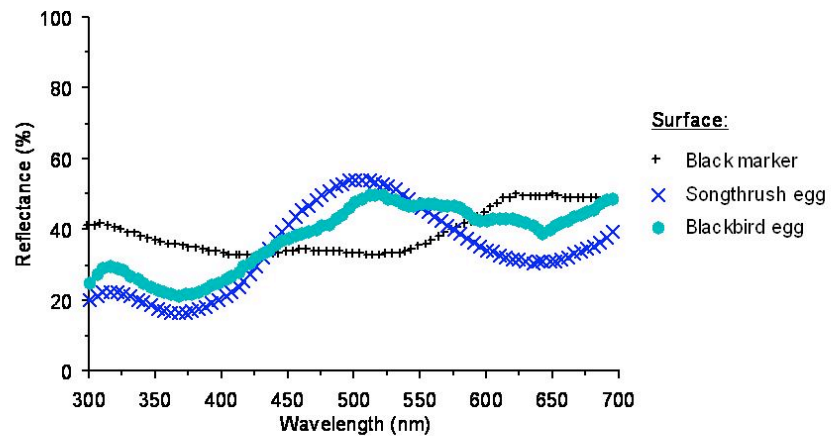
Given that clutch size of blackbirds is consistently smaller than that of song thrush, and that clutch sizes are even smaller in these *Turdus* species in their introduced range of New Zealand than in their native European range (Evans et al., 2005; Cassey et al., 2006), life history theory specifically predicts that less virulent parasitism would select for *more frequent nest desertion in blackbirds* compared to *more frequent egg ejection in song thrush* (Servedio & Hauber, 2006). Alternatively, more virulent interspecific brood parasitism would select for egg ejection in both species, irrespective of clutch size (Hauber, 2003). These predictions were tested using experimentally manipulated egg phenotypes in New Zealand, where interspecific parasitism is absent on *Turdus* spp. (Hale & Briskie, 2007).

## **Methods**

General procedures: To document behavioural tactics of egg rejection in response to experimentally manipulated coloration, *Turdus* nests were located during the laying and incubation stages to alter the appearance of one of the eggs already laid in a clutch. For this thesis chapter, I present a novel contextual framework and analyses of unpublished experimental data collected during the 2005-8 austral breeding seasons

(September – January) for both species while I was in residence in New Zealand. Introduced European blackbirds and song thrush are widespread across New Zealand and occur sympatrically in both urban and rural habitats at high densities. The study sites included urban and rural parkland within a 50 km radius of Auckland and Hamilton cities, North Island, New Zealand. *Turdus* nests are conspicuously bulky structures that can be easily noticed when searching wooded vegetation near open grasslands and lawns. Each nest was included in a single experimental procedure. Although breeding birds were not colour marked in this study, pseudoreplication was considered to be minimised by conducting experiments typically within periods of 1-2 weeks at each site, followed by a move to another study site 7+ km away, thus reducing the chance of using two nests of the same parents.

Egg manipulation protocols: At each nest, all eggs already in the nest were marked for individual identification with a black felt pen at the blunt end (to control for scent). In addition, one egg was manipulated by either (1) dyeing it with 20 black spots of approximately 4 mm in diameter, leaving the background colour visible (Fig. 2.1), or (2) dyeing it all black, covering the background colour entirely. After manipulation, the egg was returned to the clutch. This procedure avoided the use of artificial egg materials (Martin-Vivaldi et al., 2002; Moskát & Honza, 2008) by manipulating the phenotype of the hosts' own eggs (Honza et al., 2007; Moskát et al., 2008), therefore varying only the single parameter of egg coloration (Hauber et al., 2006). However, as cuckoos typically remove a host egg when laying their own egg (Davies, 2000), and so this protocol did not alter the clutch size for these experiments.



(e)

Figure 2.1. Clutches with manipulated eggs of European blackbirds (a,b) and song thrush (c,d), with representative avian-visible reflectance spectra (taken following Cassey et al., 2009) of black marker covered shell, natural blackbird egg background, and natural song thrush egg background (e). Photo credits: Mark E. Hauber.



The nest contents were then checked up to 5 days after manipulation to assess whether the manipulated egg was present or missing. Clutches in which new egg(s) appeared were considered to be during the laying stage for the experiment while all other clutches were considered to be during the incubation stage.

No unmanipulated but handled eggs disappeared. Dyed eggs that disappeared in  $\leq 5$  days (experiment = day 0) were considered ejected (Hale & Briskie, 2007) and clutches with cold or wet eggs within this period were considered deserted. Confirmed nest desertions were recorded during at least one subsequent visit to the nest. Nests with evidence of predation (i.e., broken eggs, shell remains within a cold clutch, and entirely missing clutch contents) were excluded from the analysis.

Statistical analyses: I first used nominal logistic mixed models to examine potential differences between years, study sites, and breeding stages with respect to the outcome of these experiments with either *Turdus* species. In the absence of an overall statistical effect of these predictors (see below), all data were combined into contingency analyses for each species separately.

The combined data sets were based on sample sizes which varied between 27 – 34 per taxon and per treatment, comprising some of the most extensive datasets using the same experimental methodology for egg rejection studies in any passerine bird (Grim, 2007). I then specifically examined (i) what the effects of treatment were on either bivariate and or detailed rejection responses and (ii) whether there were species-specific differences in the detailed rejection responses.

## Results

Multivariate analysis: Whether hosts accepted or rejected any of the two types of dyed eggs was not related to year of experimentation, different study sites, and the breeding stage at the time of the experimentation (nominal logistic fit model: all Wald  $\chi^2 < 0.51$ ,  $P > 0.91$ ). There was also no relationship of the same predictor variables when examining the hosts' rejection responses within the black dyed egg treatment only (all Wald  $\chi^2 < 1.6$ ,  $P > 0.44$ ). Therefore, univariate analyses are presented below for each species separately.

Rejection rates: European blackbirds rejected black eggs (67%) more often than 20 spotted eggs (13%) (Fisher's exact test [Fet]:  $P < 0.001$ ,  $n = 57$ ). Song thrushes also rejected black eggs (50%) more often than 20 spotted eggs (6%) (Fet:  $P = 0.001$ ,  $n = 64$ ). There were no species differences in either the higher rejection rates of black eggs (Fet:  $P = 0.21$ ) or the lower rejection rates of 20 spotted eggs (Fet:  $P = 0.42$ ) (Fig. 2.2).

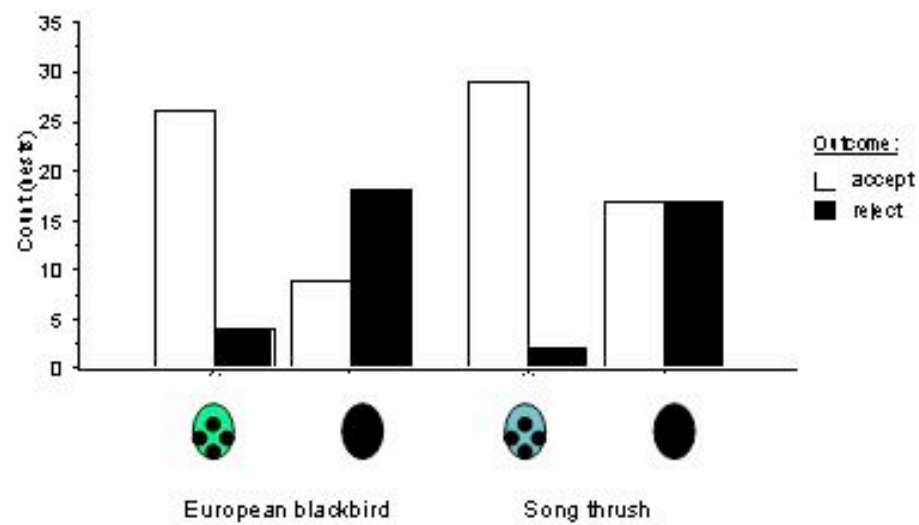


Figure 2.2. Bivariate outcomes of experiments of European blackbird and song thrush clutches in response to manipulation of single eggs

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Methods of rejection: Regarding the detailed methods of egg rejection, blackbirds ejected all ( $n = 4$ ) and song thrush either ejected (1) or deserted (1) those eggs that were rejected following the 20 spotted manipulation (sample sizes too small for a

statistical test). Blackbirds most often deserted nests with black eggs (14 of 18 rejections), whereas song thrush most often ejected black eggs (14 of 17 rejections) (Fet:  $P = 0.0006$ ) (Fig. 2.3.).

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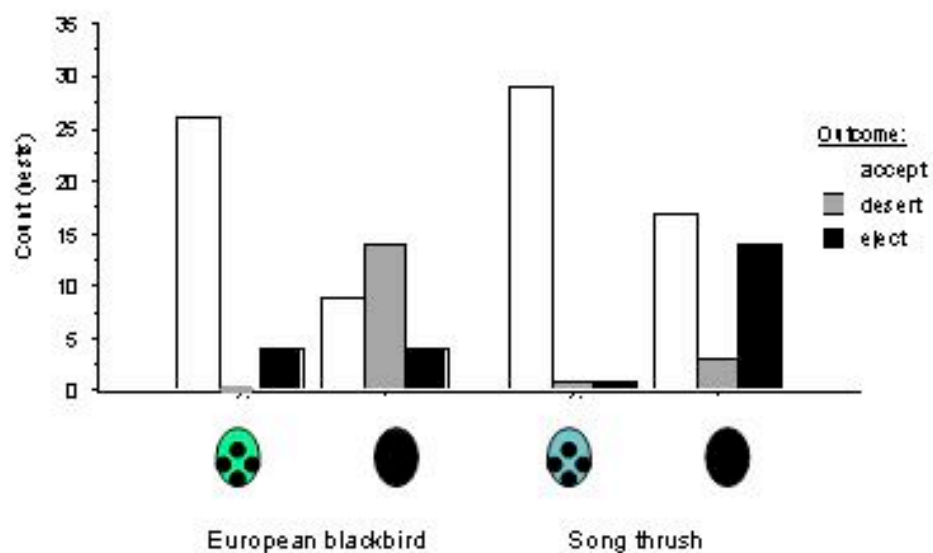


Fig. 2.3. Detailed behavioural responses of European blackbirds and song thrush in response to colour manipulations of single own eggs per clutch.

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**Discussion**

These data (Fig. 2.2) support previous work on European blackbirds, song thrush, and several other hosts of brood parasites by demonstrating that eggs whose background coloration matches that of host eggs are more likely to be accepted than eggs whose background coloration is altered dramatically (Rothstein, 1975; Davies & Brooke, 1989; Hauber et al., 2006; Rutila et al., 2006; Moskát et al., 2008). Yet, in contrast to previous work on *Turdus spp.* in both their native (Grim & Honza, 2001; Grim et al., 2011; Honza et al., 2007; Moskát et al., 2003) and introduced ranges (Hale & Briskie, 2007), here it was found that blackbirds and song thrush at the New Zealand study sites responded to non-mimetic eggs by different egg rejection methods: blackbirds typically deserted experimental clutches with black eggs while song thrush ejected black eggs and continued to incubate (Fig. 2.3). In the absence of repeated observations on the same individuals, however, we cannot conclude whether egg ejection and nest desertion are alternative strategies or tactics (*sensu* Gross, 1996) within individuals' antiparasitic behavioural repertoires of these species. We can, however, reject the hypothesis that differences in details of egg rejection methods were owing to experimental or observational variation in reproductive stage or seasonality, as neither of these predictors explained significant proportions of behavioural variability in these data. Critically, for the recognition system analysis of host-parasite coevolution in this thesis, it can also be concluded that the behavioural response of these two *Turdus* thrushes do and must include nest desertion as an alternative parasitically induced response behaviour to egg ejection in future experimental and observational studies.

These results are consistent with several scenarios for the evolution of blackbird and song thrush egg rejection behaviours. First, these data are consistent with a moderately virulent level of parasitism selecting for the species-specific egg rejection strategies of blackbirds and song thrush. Given that blackbirds have a smaller clutch size than do song thrush in New Zealand (Evans et al., 2005), life history theory predicts that in response to moderately costly nest parasitism blackbirds should be more likely to reject parasitism by nest desertion rather than egg ejection (Table 2.1, Servedio & Hauber, 2006). In fact, life history theory would also predict that any moderately costly circumstance which reduces the breeding success of nesting birds (i.e. the presence of detritus, broken shells, foreign objects, etc.) should select for nest abandonment by blackbirds compared to song thrush with their relative differences in clutch sizes (Hoover et al. 2006; Servedio & Hauber, 2006), and so behaviours unrelated to parasitism and connected with, for example, nest hygiene of broken eggshells (Hauber, 2003) and nest cleaning of non-egg materials, too, could explain the observed species-specific differences in responses to black eggs from these experiments (Moskát et al., 2002).

An alternative is that egg rejection in blackbirds evolved in response to less virulent brood parasitism compared to more virulent parasitism on song thrush. For example, intraspecific brood parasitism in blackbirds versus common cuckoo parasitism in song thrush would too predict the same alternative pattern of egg rejection behaviours that was observed in this study. That successful common cuckoo parasitism has only been recorded on song thrush and not in blackbirds in museum collections is consistent with this scenario (Grim et al., 2011).

Finally, it is possible that interspecific parasitism has less costly consequences for blackbirds than for song thrush, even when caused by virulent brood parasites. For example, cuckoo chicks do not always succeed in host nests, owing to nest architecture, host foraging regimes, and discrimination (Grim et al., 2009). Accordingly, experimental work (Grim, 2006; Grim et al., 2011) recently demonstrated that common cuckoo chicks do not survive in broods of blackbirds, thus imposing time-limited costs on the foster parents. In contrast, cuckoo chicks grow rapidly and can fledge successfully from experimental broods of song thrush, thus potentially imposing high and longer-lasting costs on the fosterers. Once again, these relative levels of virulence would predict more nest desertion by blackbirds and more egg ejection by song thrush, as documented by this study (Table 2.1). Given these parallel predictions of the alternative evolutionary scenarios, future experimental and comparative work should focus on predicting additional differences in the egg rejection behaviours of *Turdus spp.* in response to more or less virulent parasitism.

Irrespective of the evolutionary history, these data confirm that the use of birds' own eggs, together with experimental manipulation of egg appearance, can be used to effectively test alternative predictions of sensory mechanisms (Honza et al., 2007; Moskát et al., 2008) as well as life history (Servedio & Hauber, 2006) and optimal acceptance threshold theory (Hauber et al., 2006). Specifically, future work should address the range of behavioural responses and rejection repertoires of individuals and populations, following natural or experimental intraspecific brood parasitism within and outside the native ranges of blackbirds and song thrush. In addition, these data also call for further experimental work, using matched methodologies, to compare and

contrast the egg rejection behaviours of potential hosts within and outside areas of sympatry with avian brood parasites.



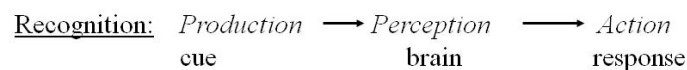
## Discussion and Implications

The overarching aim of this thesis is the use of a unified recognition systems based approach, to explore, study, and understand the processes involved in the evolutionary responses of hosts of avian brood parasites to foreign eggs in their nests. Here, the classic tripartite recognition system definition (Sherman et al., 1997) was modified by forgoing the analysis of the recognition cue itself, because that is the property of the egg of the parasite, not of the host, and instead the focus was placed on the SENSORY PROCESSES of the hosts involved in detecting the foreign egg, the COGNITIVE DECISION RULES involved in assessing and determining the response (if any) to these cues, and, finally, the BEHAVIOURAL DISPLAYS involved in responding to the foreign egg's cues (Fig. D.1).

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### Recognition Systems

**Sherman et al., 1997:**



**Host-based recognition systems approach:**

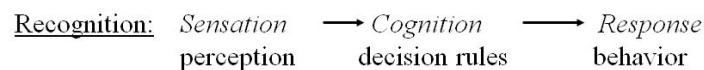


Figure D.1. Alternative constructions of a recognition systems based approach, applicable to understanding hosts' behavioural responses to foreign eggs.

The results of the experiments presented in this thesis lend strong support for the benefits of such a recognition systems based approach. Accordingly, Chapter 1 described the presence of a sensory consistency with which different egg colour manipulations played a role in perceiving foreign eggs as potentially acceptable in the nest. Importantly, the relative order of these colours eliciting rejection behaviour was irrespective of the presence of hosts' own eggs in the nest, implying that self-referencing the hosts' own eggs was not critical for the cognitive bases of these decisions. In turn, Chapter 2 clearly identified that both egg ejection and nest desertion can be experimentally induced as behavioural responses to the presence of foreign eggs in the nest. In these studies, by identifying and distinguishing the roles that sensory, cognitive, and behavioural processes play in recognizing foreign eggs, it became possible and feasible to separate potential confounds of abilities to perceive differences and evolved behavioural repertoires which in turn generated the recorded outcomes of rejection behaviours.

To illustrate the benefits of this approach, let us consider the example that, at the interspecific level, there is a long standing conundrum in that hosts of brown-headed cowbirds (*Molothrus ater*) do not reject foreign eggs even though this parasite lays a highly non-mimetic egg (Hauber, 2003). In turn, common cuckoos lay highly mimetic eggs, many of which are ejected by hosts (Moskát & Hauber, 2007) (Figure D.2).



Figure D.2. Eastern phoebes (*Sayornis phoebe*) do not reject distinctive parasitic cowbird eggs (speckled egg, left image), whereas great reed warblers reject over 30% of naturally laid mimetic cuckoo eggs (top left, right image). Photo credits: Mark E. Hauber, C. Moskát.

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In my own experience, I have found that simply talking about and presenting the findings and images from Figure D.2. often elicited statements and questions from students, colleagues, and the general public in reference to severe cognitive limitations of host birds of avian brood parasites. However, the recognition systems approach allows us to dissect this apparent sensory, cognitive, and behavioural dissonance. Accordingly, from the perspective of the sensation of the cues of hosts versus parasites, it is no surprise that visual models of the avian sensory system repeatedly confirm that differences in the background coloration and the maculation of host versus parasite eggs can be generally detected both by hosts of interspecific avian brood parasites (Stoddard & Stevens, 2010, 2011), and even by

phylogenetically related, non-host bird species and humans (Cassey et al., 2008b, 2009, 2010). Therefore, the lack of sensory discrimination does not appear to be answer the resolve the puzzle of Fig. D.2. That said, a focus on sensory processes alone results in a novel alternative proposal: instead of being moderately mimetic (Klippenstein & Sealy, 2008), perhaps cowbird eggs are simply cryptic (B. Strausberger, personal communication). This hypothesis predicts that cowbird eggs are accepted, not because they cannot be identified in comparison with the hosts' own eggs, but because they cannot be delineated and detected against the background pattern of the host nest's illumination; this hypothesis thus far remains untested in cowbirds but received support for the non-mimetic, dark eggs of *Chalcites* cuckoos in Australia (Langmore et al., 2009).

The experimental design and the results of Chapter 1 provide further support for this approach. Despite the scenario depicted in Fig. D.2., extensive previous work on the sensory basis of host-parasite egg rejection, conducted using subjects within the same species, consistently supported the pattern that increasing mimicry leads to reduced rejection (Hauber et al., 2006; Rutila et al., 2006). However, in most of these studies only a single foreign egg was introduced into experimental nests, thereby confounding the sensory mechanisms of concurrent contrast of own versus foreign eggs and sensory filters assessing the sensory inputs from the foreign egg alone. Therefore, to disentangle these confounding factors, experimental tests of the sensory mechanisms of rejecter hosts require nest manipulations where the entire clutch has been altered. Recently, Moskát et al. (2010) conducted such a set of experiments, where all eggs in great reed warblers' nests were manipulated and found that egg rejection rates increased above background/control levels. Still, even in that experiment, all host

eggs were manipulated in the same way, so that the sensory threshold of acceptance versus rejection could not be tested. Therefore, in Chapter 1 the experimental paradigm included an all-clutch manipulation where each of the hosts' five eggs was dyed with different colours. The results of the absolute rejection rates showed consistent decreases from single-egg to the five-egg treatments. In contrast, the relative rejection rates of the specific colours remained consistent between the single-egg and the five-egg experiments in that blue eggs were accepted the most and orange eggs were accepted the least often. The conclusion is that these hosts possess a consistent ordinal acceptance thresholds to detect foreign egg colours, but whether those foreign eggs elicit responses, and are behaviourally rejected, may be modified by context, including the proportion of hosts' own eggs present in the nest.

The critical conclusion from Chapter 1 is, thus, that hosts recognize more eggs than they actually reject. This conclusion also has implications for the second component of the recognition systems approach, the cognitive decision rules involved in mediating behavioural responses through sensation and perception. Specifically, in contrast to the opinion of those sceptic audience members in response to my presentation about complex avian cognition (Fig. D.2., see above), the new results reveal that the lack of behavioural responses to foreign eggs cannot be considered as necessarily being due to cognitive limitations of host birds (Antonov et al., 2009; Moskát & Hauber, 2007).

The final component of the recognition systems approach is the analysis of the behavioural responses to foreign eggs by potential hosts of brood parasites. Although focusing on a different set of egg rejecter species, Chapter 2 also represents a novel

contribution of the analyses of the variation in the repertoire of behavioural responses to foreign egg colours. This is because the experimental outcomes of this study established nest desertion behaviours in response to egg manipulation as specifically induced behavioural outcomes, relative to control manipulations. This is in sharp contrast with the analytical approaches of many other studies, in which nest desertion was not seen as an evolved response to brood parasitism (Chapter 1). The conclusion is that nest desertion must be examined in detail and taken into consideration when analyzing the outcomes of new experiments with *Turdus* thrushes, as well as when interpreting the results of published studies with congeneric thrush species (Grim et al., 2011; Hale & Briskie, 2004; Moskát et al. 2003).

The broader implication of the range of experimental methods presented in this thesis, including the critical uses of parallel and concurrent manipulations, is that these experimental manipulations can provide the basis of several parallel experiments using photographic/image presentation approaches in an odd-one-out paradigm. Below is a schematic (Fig. D.3) and a set of representative test-images of just such an experimental design. In this experiment, a set of reference images would be provided to the subjects to familiarize them with the range of acceptable eggs (images with clutches of host eggs only), thereby providing a range and variation of acceptable phenotypic traits present in the population.

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	Reference image to identify parasite eggs	Experimental image contains	"Parasite" egg identity	Predicted outcome: Discordancy	Predicted outcome: Conspecific familiarity
		Host eggs only	None	None	None
		1 cuckoo and 6 host eggs	Cuckoo egg (left most egg)	Cuckoo egg	Cuckoo egg
		1 dyed and 3 host eggs	Dyed egg	Dyed egg	Dyed egg
		4 dyed and 1 host egg	All dyed eggs	Host egg	Dyed egg
		All dyed eggs	All eggs	None	Dyed egg

Figure D.3. The schematic of an experimental paradigm and the predicted responses to detect foreign eggs based on concurrent alternative manipulations of clutch content.

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Following the familiarization step (top row), a novel set of images would then be provided (ideally, standardized for egg size and clutch size: number of eggs) and the subjects would be asked (people) or trained (non-human animals) to detect and point to the foreign egg. By using a suite of different clutch images, with natural or artificially manipulated foreign egg(s) placed in the nest, including either single

foreign eggs or multiple (including all) foreign eggs in the clutch, the concurrent experimental approach advocated here, modified from Moskát et al. (2010) and Chapter 1, could be applied into this paradigm. The representative study illustrated above, for example, could focus on cognitive mechanisms based on discordancy (i.e. the detection of the odd-egg, relative to the majority egg type present in the nest) versus conspecific familiarity (i.e. the detection of eggs with an unfamiliar phenotypic trait, which would fall outside the range presented during the familiarization stage of the experiment using acceptable, conspecific eggs only). Because these cognitive mechanisms make different predictions about the eggs identified as foreign during the experiment (Fig. D.3., right hand two columns), it will be possible to identify which algorithm is used the subjects to recognize foreign eggs.

Critically, a second conclusion associated with the schematic and the predictions of this experimental design, is that experiments with natural or artificial cuckoo eggs, which are based on the presence or the introduction of a single parasitic egg in the nest, cannot be used to discriminate between the specific alternative cognitive decision rules whose predictions are illustrated in Fig. D.3 and make the same predictions for the middle-two row of experiments. Instead, to contrast the predictions of these alternatives, it is required that additional manipulations of several eggs in each clutch take place (bottom two rows, contrasting predictions). Furthermore, by altering the relative proportion of host versus foreign eggs, or changing the absolute number of host and foreign eggs in the nest, this experimental schematic will also be feasible to identify and test specific predictions of alternative, hypothesized or novel cognitive mechanisms, not previously identified in rejection decisions hosts of obligate avian brood parasites (e.g., numerosity of host versus parasite eggs: Low et



al., 2009; Lyon, 2003; White et al. 2009). For example, some host species are poorer at identifying foreign eggs in the nest with increasing number of their own eggs, because more eggs represent greater phenotypic variability against which foreign eggs are compared, as predicted by each or a combination of the discordancy-, familiarity-, and internal template-based mechanisms (Moskat & Hauber, 2007; Moskát et al., 2008c, 2009). To discriminate between these alternatives again requires a concurrent experimental design suitable for the schematics presented in Fig. D.3.

The main conclusion of this thesis is that future work should incorporate both the conceptual and the practical details developed in the studies here in order to better understand the evolutionary parallels and innovations required to detect parasitic eggs. In addition, it is essential to examine concurrently whether multiple cognitive processes are involved in the behavioural discrimination of own and foreign eggs, for instance discordancy and self-referenced familiarity. Yet, in the absence of the availability of either of these mechanisms, an internal threshold-based discrimination decisions may also be available to hosts detect foreign eggs; the combination of these non-mutually exclusive alternative cognitive processes can clearly produce efficient and beneficial rejection decisions. That cognitive mechanisms do not act mutually exclusively, but instead supplement and combine with each other, is consistent with the scenario that increasingly fail-safe mechanisms of accurate parasite-egg detection function in these hosts (Hauber & Sherman, 2001; Moskát et al., 2010). Future work, therefore, should also examine the novel prediction whether the evolutionary response to arms-races with increasingly mimetic hosts may be the concurrent reliance on multiple cognitive decision rules to converge on the detection of and the behavioural decision to reject the foreign egg(s) from the nest.

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