http://researchcommons.waikato.ac.nz/

Research Commons at the University of Waikato

Copyright Statement:

The digital copy of this thesis is protected by the Copyright Act 1994 (New Zealand).

The thesis may be consulted by you, provided you comply with the provisions of the Act and the following conditions of use:

- Any use you make of these documents or images must be for research or private study purposes only, and you may not make them available to any other person.
- Authors control the copyright of their thesis. You will recognise the author’s right to be identified as the author of the thesis, and due acknowledgement will be made to the author where appropriate.
- You will obtain the author’s permission before publishing any material from the thesis.
Suboptimal Choice Behaviour in Hens

A thesis
submitted in partial fulfilment
of the requirements for the degree
of
Masters of Applied Psychology in Behaviour Analysis
at
The University of Waikato
by
KARMEN LOUISE NGATAI

THE UNIVERSITY OF WAIKATO
Te Whare Wānanga o Waikato

2013
Abstract

Choice performances of six Brown Shaver hens were studied across three series of conditions, using a partial replication of Stagner and Zentall’s (2010) procedure. Hens chose between two alternatives during choice-trials. Choice of the low-probability alternative provided one of two stimuli that reliably predicted 100% reinforcement on 20% of the trials, and 0% reinforcement on the remaining 80% of trials. Choice of the non-discriminative alternative provided one of two unreliable stimuli that non-differentially signalled 50% reinforcement, regardless of the stimulus presented. In Conditions 1-4 and Condition 6, the stimuli and reinforcement contingencies associated with the side keys were repeatedly reversed across conditions. In Condition 5, stimulus and reinforcement contingencies were each equated at 50%. Results replicated Stagner and Zentall’s (2010) findings demonstrating that choice for the low-probability alternative for most hens remained almost exclusive across reversals, except Condition 5 where previous choice performances for all subjects, was disrupted. In Conditions 7-11, the reliability of the low-probability stimuli was gradually decreased across conditions. Results showed that the decreasing reliability of the low-probability stimuli did not deter many hens from choosing suboptimally. Conditions 12 and 13 reversed Conditions 8 and 11, respectively. Results showed that choice performances for most hens in Condition 13 varied considerably from Condition 11. The main finding from this study is that hens do not exclusively choose signals that reliably signal a reinforcing outcome. This is because choice for the low-probability alternative for many hens was not affected when the reliability of those signals decreased. This suggests that the signals themselves may be more reinforcing than their subsequent outcome which may have implications for human gambling behaviour.
Acknowledgements

A huge thank you goes to my unbelievably insightful (and humorous) supervisors, Drs Lewis A. Bizo and James S. McEwan, for their guidance, support, and assistance throughout this academic adventure that is a thesis; your unwavering calm and encouragement has made this a totally enjoyable experience. I am especially thankful for all those little life-lesson-reminders you both managed to instil in me along the way. The extensive knowledge I have gained from you, both academically and in life, are invaluable and I look forward to sharing and applying that knowledge in the future.

Special thanks to Jenny Chandler for all her technical support and expertise, and for her continued education regarding animal welfare (and their diverse personalities), and tending to my ladies (the 12s). Many thanks to my fellow students at the Animal Behaviour and Welfare Research Unit, without whom there would be no data for this thesis. Thank you all for running my experiment and helping me with the data collection process. I especially want to thank you for your friendship and support; I have learnt so much from each of you, and have made some life-long friends during my time here. I wish you all the very best in completing your theses/PhDs, and every success for your future.

To my closest friends, who always knew when to kidnap me away from my studies, and who persisted every time I said ‘no’ to their invites – thank you for your and patience! Thanks also for sharing the tears and laughter, and the tears from laughing so much – you all kept me (in)sane throughout this crazy journey.

Extra special thanks to my study-buddy, Miss Lottie (the possum), who kept me entertained, awake and on my toes during the many long nights it took to write this thesis. You will be missed!
Dedication

This thesis is dedicated to my family and my daughter, Ciarne, who not only instigated this journey, but has continued to inspire me every step I have taken along the way.

To my family; words cannot begin to express my love and appreciation to you all, for your enduring and unwavering emotional and financial support, encouragement, and belief in me, and your humour. You truly are my backbone and the source of my strength and determination! I am so very grateful and honoured that you were with me every step of the way throughout this incredible journey. We’re finally here – we made it! Love you loads xx

To my daughter, Ciarne; thank you for your laughter, your smiles, hugs, and your patience (especially when I had my own tantrums). Thank you also for the endless supply of amazing coffees you made me over the years, and the many times you put the lids back on my highlighters and threw a blanket over me whenever I fell asleep in the midst of studying.

Most of all, I want to thank you for making me stop, for reminding me to play, and to enjoy those moments of calm and quietness during the most difficult and stressful times. You have brought me absolute joy every day of your 14 years, and you truly are my inspiration for my being all that I am and the best I can be! I am so very honoured and grateful that you were right beside me on this path that I chose for us. I only hope that this has encouraged you to walk your own path to success; and know that wherever that path takes you, I will be right beside you every step of the way. I love you my cub! xx
# Table of Contents

Abstract ............................................................................................................................ ii

Acknowledgements .......................................................................................................... iii

Dedication ........................................................................................................................ iv

Table of Contents ........................................................................................................... v

List of Tables .................................................................................................................... viii

List of Figures ................................................................................................................... ix

List of Appendices .......................................................................................................... xi

Introduction:

Human and Animal Gambles......................................................................................... 1

Investigating Choice ....................................................................................................... 5

Concurrent Chains Procedure ...................................................................................... 5

Hysteresis ....................................................................................................................... 7

Observing Responses: Choice for Reliable Signals? ..................................................... 8

Saliency of Discriminative Stimuli:

Information Theory ....................................................................................................... 10

Conditioned Reinforcement Theory ........................................................................... 12

Contrast ......................................................................................................................... 12

Delay Reduction Theory ............................................................................................. 15

Animal Models of Human Gambling ........................................................................... 18

Accounting for Suboptimal Choice:

Positive Contrast .......................................................................................................... 25

Certainty of Reinforcement ......................................................................................... 27

Ambiguity-Aversion ...................................................................................................... 28
Conditioned Reinforcement and Observing Behaviour .................. 31
The Experiment: An Investigation of Suboptimal Choice Behaviour .... 34
Replication Series (Conditions 1-6) ............................................ 35
Reliability of Stimuli Series (Conditions 7-11) .............................. 36
Controls for Bias Series (Conditions 12 and 13) ........................... 37
Method ...................................................................................... 39
Subjects .................................................................................... 39
Apparatus .................................................................................. 40
Procedure .................................................................................. 41
General Procedure ........................................................................ 43
  Pairing of Stimuli ....................................................................... 43
  Presentation Probabilities of Stimuli ........................................... 44
  Probabilities of Reinforcement ................................................ 44
  Terminology for the two Alternative Schedules .......................... 45
  Chained Procedure ..................................................................... 45
The Experiment ............................................................................ 46
  Reinforcement Ratios .................................................................. 46
  Forced-Choice Trials .............................................................. 47
  Choice-Trials ............................................................................. 48
  Terminal-Link Outcomes ......................................................... 48
Procedure for Conditions 1-6 (Replication Series) ....................... 49
Procedure for Conditions 7-11 (Reliability of Stimuli Series) ........... 55
Procedure for Conditions 12 and 13 (Controls for Bias Series) ........ 61
Results.................................................................................................................................68

Results for Conditions 1-6 (Replication Series).................................................................69

Results for Conditions 7-11 (Reliability of Stimuli Series)..............................................74

Results for Conditions 12 & 13 (Controls for Bias Series).............................................79

Discussion ...........................................................................................................................87

Discussion for Replication Series (Conditions 1-6).......................................................87

Discussion for Reliability of Stimuli Series (Conditions 7-11).................................91

Discussion for Controls for Bias Series (Conditions 12 & 13).................................93

General Discussion........................................................................................................98

Appendix A ..................................................................................................................107

Appendix B ..................................................................................................................108

Appendix C ..................................................................................................................109

References ....................................................................................................................110
List of Tables

Table 1. Free-feeding and running weight averages (+/- 2gms), for each hen, including average free-feeding weight percentages, and standard deviations.................................................................40

Table 2. Order of experimental Conditions 1-6 showing the presentation probability of each stimulus in each alternative, its corresponding probability of reinforcement, and the side key that each alternative was presented on, for each condition .................................................................................................................. 51

Table 3. Number of sessions each subject experienced in Conditions 1-6........52

Table 4. Order of experimental Conditions 7-11 showing the presentation probability of each stimulus in each alternative, its corresponding probability of reinforcement and reinforcement ratio for each condition....................................................... 59

Table 5. Number of sessions each subject experienced in Conditions 7-11...... 60

Table 6. Order of experimental Conditions 12 and 13 showing the presentation probability of each stimulus in each alternative, its corresponding probability of reinforcement and reinforcement ratio for each condition....................................................... 66

Table 7. Number of sessions each subject experienced in Conditions 12 and 13..........................................................................................................................67
List of Figures

Figure 1. General procedure used in this experiment (Stagner & Zentall, 2010) ................................................................. 21

Figure 2. Results from Stagner and Zentall’s (2010) study ..................................... 24

Figure 3. Diagram of the complete series of choice procedures for experimental Conditions 1-6................................................................. 50

Figure 4. Diagram of the complete series of choice procedures for experimental Conditions 7-11................................................................. 58

Figure 5. Diagram of the choice procedures for experimental Conditions 12 and 13................................................................. 65

Figure 6. Percentage of choice responses for the low-probability (20%) or left-key alternative of reinforcement, over a non-discriminative alternative of 50% reinforcement, plotted across consecutive sessions for each hen across Conditions 1-6................................................. 70

Figure 7. Percentage of choice responses for the low-probability alternative of 20% reinforcement over a higher, non-discriminative alternative of 50% reinforcement, plotted across consecutive sessions for each hen across Conditions 7-11......................... 76
Figure 8. Percentage of choice responses for the low-probability alternative of 20% reinforcement over a higher, non-discriminative alternative of 50% reinforcement, plotted across consecutive sessions for each hen across Conditions 11-13................. 81
List of Appendices

A. Excel files with a summary of raw data ......................................................... 107

B. Hen weights and post-feed amounts during experimentation ..................... 108

C. Ethics approval (protocol number: 870)......................................................... 109
Introduction

Human and Animal Gambles

Human gambling generally involves a suboptimal choice to forego money in one’s pocket for the low-probability of winning more (Zentall & Stagner, 2011b). In particular, human gamblers often choose a low-probability but high-payoff alternative, over a high-probability but low-payoff alternative – such that over time, the net expected return is less than what the gambler has wagered overall (Molet et al., 2012; Rachlin, 1990; Zentall, 2011; Zentall & Laude, 2013; Zentall & Stagner, 2011a). Such gambles are typical of casino games such as slot machines, black jack and roulette, or when one plays Bingo, and are especially true when one regularly buys ‘scratchies,’ lotto and monetary raffles. Thus, the long-term consequence of repeated gambles results in more losses than wins.

Having sufficient experience with their ‘game of choice’ means the gambler can adequately learn about the low-probability of winning, but this does not appear to reduce the frequency of gambling behaviour (Zentall, 2011; Zentall & Stagner, 2011a). Ironically, losses may well increase the gambler’s propensity to gamble and thus maintains gambling behaviour (e.g., the near win effect, Kassinove & Schare, 2001; Rachlin, 1990; Reid, 1986; Turner, Zangeneh, & Littman-Sharp, 2006; Weatherly, Sauter, & King, 2004; and see Magalhaes, White, Stewart, Beeby, & van der Vliet, 2012; Navarro & Fantino, 2005, for the sunk cost effect).

The continued engagement in gambling despite increasing losses suggests that human gamblers not only fail to maximise their gains and minimise their losses (de Villers, 1977; Laude, Beckmann, Daniels, & Zentall, 2013), they also tend to overvalue their wins, and discount their losses (e.g., the availability heuristic, Tversky
& Kahneman, 1974; see also, Rachlin, 1990). A possible explanation for this bias was proffered by Breen and Zuckerman (1999) who reported that wins are more salient to gamblers than their more frequent losses (see also, Rachlin). In terms of public gambling, this concept could not be more true. When someone wins at a casino, the win is usually reinforced with combinations of flashing lights, ringing bells and social attention (Breen & Zuckerman, 1999; Madden, Ewan, & Lagorio, 2007; Petry, 2005; Zentall, 2011), whereas losses are not. An argument could be made, however, that losses potentially motivate more gambling so as to obtain the win (Kassinove & Schare, 2001; Navarro & Fantino, 2005; Rachlin).

By contrast, animals should be less susceptible to suboptimal choices analogous to that shown by humans when they gamble. This is because their survival is likely to be dependent on the animal engaging in optimal foraging behaviours (Stephens & Krebs, 1986). According to optimal foraging theory, animals should make optimal choices with regard to food acquisition because natural selection generally favours the survival of animals that engage in such behaviours (Stephens & Krebs; see also, Bell & Baum, 2002; MacArthur & Pianka, 1966). It is also thought that animals are sensitive to the relative amounts of food (or rewards) that can be obtained from different alternatives (or food sources), provided they have had appropriate experience with those options (de Villers, 1977; Fantino & Abarca, 1985). For example, Fantino and Abarca (1985) reported that animals maximise reinforcement by choosing the alternative that provided the most reinforcement regardless of whether it was the rate, amount or probability of reinforcement that was manipulated (see also, Autor, 1969; Herrnstein, 1964).

In terms of an analogy to human gambling, optimal foraging theory would therefore hold that when given a choice between different probabilities of
reinforcement, animals should be less likely to choose the alternative associated with less reward (i.e., gamble). By default, animals are more likely to choose the optimal alternative associated with the greatest probability or quantity of food (i.e., not gamble). In contrast to human gambling behaviour, this would suggest that animals should maximise gains – not gamble – and minimise losses (e.g., gamble; Laude et al., 2013). Paradoxically however, this is not the case.

Recent research has shown that rats (e.g., Rivalan, Ahmen, & Dellu-Hagedorn, 2009; Zeeb, Robbins, & Winstanley, 2009) and pigeons (e.g., Gipson, Alessandri, Miller, & Zentall, 2009; Stagner & Zentall, 2010; Zentall & Stagner, 2011a) are susceptible to choosing suboptimally in choice procedures that simulate human gambling behaviour. In particular, many studies have consistently shown that pigeons prefer stimuli that reliably predict the presence (S+) and absence (S-) of a low-probability but high payoff alternative, where the loss of food occurred with greater frequency (i.e., gambling-like alternative), over stimuli that non-differentially signalled a high-probability but low payoff alternative which provided more food overall (i.e., optimal alternative; Gipson et al.; Laude et al., 2013; Laude, Pattison, & Zentall, 2012; Stagner, Laude, & Zentall, 2011; Stagner, Laude, & Zentall, 2012; Stagner & Zentall, 2010; Zentall, 2011; Zentall & Laude, 2013; Zentall & Stagner, 2012; see also, Belke & Spetch, 1994; Fantino, Dunn, & Meck, 1979; Mazur, 1996; Spetch, Belke, Barnet, Dunn, & Pierce, 1990). Clearly this finding is contrary to optimal foraging theory where the animal’s survival and sensitivity to different food amounts would dictate that they choose the optimal alternative (i.e., not gamble) over the gambling-like alternative (Bell & Baum, 2002; MacArthur & Pianka, 1966; Stephens & Krebs, 1986; see also, Fantino & Abarca, 1985).

This finding – that pigeons show similar suboptimal choice behaviour to
humans in gambling-like situations – suggests that the behavioural processes responsible for choosing suboptimally under comparable conditions may be similar for both species (Molet et al., 2012; Zentall, 2011; Zentall & Stagner, 2011a). As previously mentioned, wins were found to be more salient to human gamblers than losses (Breen & Zuckerman, 1999; Rachlin, 1990), and many studies show that pigeons prefer stimuli that reliably predict the presence and absence of a low-probability of reinforcement, even though it is associated with less food (Gipson et al., 2009; Stagner et al., 2012; Stagner & Zentall, 2010; Zentall, 2011; Zentall & Stagner, 2012). Based on these findings, it appears that one commonality similar to both species is that they seem to attend to the signals for ‘winning’ (reinforcement or reward), rather than the global amount of reinforcement (or reward) that is actually obtained (or lost for that matter, via their attendance to those signals rather than their subsequent outcomes; Breen & Zuckerman; Gipson et al.; Zentall, 2011; Zentall & Laude, 2013; Zentall & Stagner, 2011a).

If this speculation is correct, further investigation of animal models of gambling behaviour is warranted because it may provide valuable insights into the basic behavioural mechanisms that could contribute to, or discourage humans from, gambling (Madden et al., 2007; Peters, Hunt, & Harper, 2010; Potenza, 2009; Zentall, 2011). In addition, the finding that animals, like humans, perform suboptimally in human gambling-like choice procedures, suggests that these mechanisms can be studied more easily with animals (Madden et al.; Peters et al.; Zentall, 2011). More importantly, the investigation of suboptimal choice behaviour by animals, using an animal analogue of gambling, would specifically reduce the possibility of unintentional social, cultural, experiential and other inherently unique human biases, that may interact with the behavioural mechanisms that are thought to underlie human

**Investigating Choice**

*Concurrent Chains Procedure.* Choice behaviour in animals has been studied extensively using variations of the concurrent chains procedure (e.g., Autor, 1969; Belke & Spetch, 1994; Fantino, 1969; Herrnstein, 1961; Lalli & Mauro, 1995; Spetch et al., 1990; Spetch, Mondloch, Belke, & Dunn, 1994; Stagner & Zentall, 2010; Zentall & Stagner, 2011a). In this procedure, the subject is simultaneously presented with two (or more) concurrently available schedules of reinforcement on different response keys. The availability of the concurrent schedules are typically signalled by stimuli (e.g., the response keys could be illuminated white or with different shapes), and are called the initial-link or choice phase of the chain (Lalli & Mauro).

Initial-links are usually correlated with an equal and independent response requirement (e.g., a single response or fixed-ratio 1, FR 1). Once an initial-link has been entered, the other response key becomes dark and inoperative. When the response requirement has been met on either one of the initial-links, the subject is reinforced by a change in key colour (e.g., from white to another colour), and one of two mutually exclusive reinforcement schedules are made available during the terminal-link or outcome phase of the chain (Spetch et al., 1990).

Terminal-link stimuli are often arranged according to a fixed-time (FT) schedule, and each stimulus can be manipulated so that it either differentially or non-differentially signals the outcome to follow (Spetch et al., 1990). Terminal-link outcomes typically end with a period of access to reinforcement (e.g., food) or a blackout period (i.e., no food). Once the terminal-link outcome has been provided,
the initial-links are reinstated, and a new trial begins (Lalli & Mauro, 1995). Thus, the name of the procedure reflects the chain of events that are assigned to each alternative: The initial-link schedule provides access to the terminal-link schedules (rather than the specific reinforcer) which in turn, provides access to an outcome and together, the events constitute a chained procedure (Grace & Hucks, 2013; Lalli & Mauro).

There are many dimensions of reinforcement that can be manipulated in the terminal-links of a concurrent chains procedure such as delay (e.g., Belke & Spetch, 1994; Dunn & Spetch, 1990; Fantino & Abarca, 1985; Mattson, Hucks, Grace, & McLean, 2010; Mazur, 1996; Spetch et al., 1990; Zentall & Stagner, 2011b), magnitude (e.g., Zentall & Stagner, 2011a), or probability (e.g., Gipson et al., 2009; Stagner & Zentall, 2010). A common manipulation in the terminal-links is that one alternative usually provides reliable stimuli that differentially predicts the presence (S+) and absence (S-) of reinforcement (i.e., signalled alternative), while the other alternative does not (i.e., unsignalled alternative; Spetch et al., 1990). For example, in a signalled alternative, reliable stimuli can differentially predict whether food (S+) or a blackout (S-) will occur (e.g., 100% reinforcement), whereas unsignalled alternatives use unreliable stimuli that non-differentially signal the outcomes that may occur (e.g., sometimes food, or a blackout). Another variation of this procedure is that one alternative usually provides an overall higher probability of reinforcement than the other (e.g., Lalli & Mauro, 1995; Spetch et al., 1990; Spetch et al., 1994; see Zentall, 2011, for a review).

To ensure subjects sample the contingencies of reinforcement associated with each alternative, many studies in this area randomly intersperse forced-choice trials with choice-trials (e.g., Laude et al., 2012; Stagner et al., 2011; Stagner et al., 2012;
Stagner & Zentall, 2010). In forced-choice trials, only one alternative is available and the subject is forced to sample its corresponding reinforcement contingencies, whereas choice-trials provide the subject with a choice between those alternatives. Preference for one alternative over another is measured by the proportion of responses made to its associated initial-link key during choice-trials (Grace & Hucks, 2013; Lalli & Mauro, 1995; Mattson et al., 2010).

**Hysteresis.** Preference can also be visually determined by examining the presence of hysteresis in the data. Hysteresis is the behavioural transition from one stable state of responding to another, once a change in contingencies has been implemented (Davidson & Baum, 2000; Mazur, 1997). Thus, a comparison of the previous stable state of responding, and the transitional gradient, length and stabilisation of responding following a condition change, provides a straightforward, visual representation of the strength of a subject’s preference for one alternative over another (Davidson & Baum; Mazur). For example, a short transitional period from an old, to a new stable state of responding suggests a strong preference for one alternative over another, while longer transitions suggest a weaker preference for it.

To summarise, the use of a concurrent chains procedure means that various dimensions of reinforcement (e.g., delay, magnitude, or probability) including signalled and unsignalled outcomes, can be arranged on a chain. More importantly, the combined effects of these dimensions on choice behaviour can be investigated simultaneously using responses made to each alternative’s respective initial-link key during choice trials (Mattson et al., 2010). Similarly, the presence of hysteresis in the data provides an alternative measure of preference once a change in contingencies has been implemented.
**Observing Responses: Choice for Reliable Signals?**

When behaviour produces stimuli that reliably signals the presence (S+) or absence (S-) of reinforcement without directly affecting the overall probability of reinforcement, it is referred to as an observing response (Gipson et al., 2009; Mazur, 1996; Stagner & Zentall, 2010; Wyckoff, 1952). This is a response that effectively changes an unsignalled (i.e., mixed) condition, to a signalled (i.e., multiple) condition thus indicating which schedule is currently in effect (Mazur, 1996). For example, Wyckoff (1952) reported that pigeons would step on a treadle, the sole function of which, was to produce stimuli that differentially signalled whether reinforcement was currently available (S+) or not (S-).

In another experiment, Roper and Zentall (1999) investigated observing behaviour across a range of overall probabilities of reinforcement (e.g., 12.5%, 50%, and 87.5% reinforcement). A two-alternative concurrent chains procedure was used. Each alternative was associated with reliable (discriminative alternative) or unreliable (non-discriminative alternative) stimuli, and the same probability of reinforcement. Pigeons were randomly grouped into each reinforcement level, and they chose between the two options during choice trials. Choice of the discriminative alternative resulted in a pair of stimuli that reliably predicted 100% reinforcement (e.g., S+, a circle) or 0% reinforcement (e.g., S-, a dot). Choice of the non-discriminative alternative provided one of two unreliable stimuli (e.g., a vertical or horizontal line) that non-differentially signalled 50% reinforcement (Roper & Zentall).

Under this arrangement, pigeons showed a strong suboptimal preference of 92.5%, for the discriminative alternative that reliably predicted the presence (S+) and absence (S-) of reinforcement, regardless of the overall probability of reinforcement (Roper & Zentall, 1999). Interestingly, they found that preference for this alternative
was highest (98%), when the overall probability of reinforcement was lowest (12.5% reinforcement). Conversely, preference for the discriminative alternative was lowest (68.4%), when the overall probability of reinforcement was highest (87.5% reinforcement; Roper & Zentall).

When Roper and Zentall (1999) included a titrated response requirement to produce the reliable stimuli on the discriminative alternative, relative to a single response requirement on the non-discriminative alternative, they found that FR ratios could be increased to as much as 16:1 before preference for the discriminative alternative decreased (Experiment 2). For example, at FR 16, preference for the discriminative alternative remained relatively high for those pigeons in the 12.5% reinforcement group where mean choice for this alternative was 71.6% (Roper & Zentall, Experiment 2). This finding suggests that, not only did this group of pigeons work harder to obtain the discriminative stimuli, but by doing so, the delay to obtaining reinforcement on this alternative almost doubled (Roper & Zentall, Experiment 2). In contrast, pigeons in the 50% and 87.5% reinforcement groups showed a clear preference reversal for the discriminative alternative at FR 16, where mean choice for the non-discriminative alternative increased to 95.3% and 99%, respectively, for each group (Roper & Zentall, Experiment 2).

Both studies (Roper & Zentall, 1999; Wyckoff, 1952) provide clear evidence that animals prefer stimuli that reliably predict the presence (S+) and absence (S-) of reinforcement, over unreliable stimuli that non-differentially signal reinforcement. In addition, both studies show that animals are willing to work (e.g., stepping on a treadle, Wyckoff; or producing an increasing response requirement, Roper & Zentall) to obtain those signals. Of particular interest however, was Roper and Zentall’s (1999) finding that the lowest-probability of reinforcement produced the highest
preference for discriminative stimuli which in many cases, remained high across increasing FRs in Experiment 2 of their study.

Two popular explanations have been proposed to account for this finding. The first is that animals value the ‘information’ provided by discriminative stimuli because they reliably predict the presence (S+) and absence (S-) of reinforcement (Berlyne, 1957), rather than the absence of information which is characteristic of unreliable stimuli (Zentall & Stagner, 2012). The second more commonly accepted explanation for the strong preference for discriminative stimuli, is founded upon the principles of conditioned reinforcement (Dinsmoor, 1983). Other explanations include the concept of contrast, and delay reduction theory (e.g., Fantino, 1969; Roper & Zentall; Singer & Zentall, 2011; Williams, 2002; Zentall & Singer, 2007).

**Saliency of Discriminative Stimuli: Information, Conditioned Reinforcement, Contrast or Delay Reduction?**

Information Theory. According to information theory, when the presence and absence of reinforcement is equally likely, the amount of information transmitted by the discriminative stimuli is a function of the degree to which they reduce the uncertainty of the reinforcement schedule in effect (Berlyne, 1957). For example, in Roper and Zentall’s (1999) study, one group of pigeons were exposed to an overall probability of 50% reinforcement for each alternative. At the time of choice, the expected outcome was completely uncertain (50% reinforcement). Following choice of the discriminative alternative, the expected outcome either increased from 50% reinforcement (i.e., uncertainty) to 100% reinforcement (i.e., certainty) when reinforcement was obtained. Alternatively, expectation decreased from the uncertainty of 50% reinforcement, to the certainty of 0% reinforcement when
reinforcement was absent (Roper & Zentall, 1999; see also, Stagner et al., 2011; Stagner & Zentall, 2010). Thus, at the time of choice, the uncertainty of reinforcement on this alternative was greatest, but the information provided by the discriminative stimuli with regard to the presence (S+) and absence (S-) of reinforcement would have been of maximum value, because the signals greatly reduced the uncertainty of the schedule in effect (e.g., 100% or 0% reinforcement; Roper & Zentall).

Information theory also predicts that any additional manipulation to the overall probability of reinforcement from 50% should reduce the amount of information provided by the discriminative stimuli. For example, when the occurrence of the discriminative stimuli are equally likely, signals that reliably predict the presence (S+) of reinforcement should provide as much information as the signals that reliably predict the absence (S-) of reinforcement. When the overall probability of reinforcement associated with these stimuli are manipulated from 50%, the reliability of those signals decrease, and uncertainty as to whether reinforcement is forthcoming or not, increases (Zentall & Stagner, 2012). As a result, preference for this alternative should decline because the reduction of information provided by the appearance of the discriminative stimuli in this context, would elicit little observing behaviour (Roper & Zentall, 1999; Stagner et al., 2011; Stagner & Zentall, 2010).

Consistent with information theory, was Roper and Zentall’s (1999) finding that when the overall probability of reinforcement was highest, preference for the discriminative alternative was lowest (Experiment 1). Contrary to information theory however, was their finding that when the overall probability of reinforcement was lowest, preference for the discriminative alternative was highest (Experiment 1). This was indeed an unexpected finding. According to information theory, when the
probability of reinforcement is low, the researchers *should* have found a weaker preference for the discriminative alternative because the expectation of reinforcement was unlikely in this schedule, and was generally not obtained (Roper & Zentall; Stagner & Zentall, 2010; Zentall, 2011). But this was not the case.

*Conditioned Reinforcement Theory.* An alternative explanation for Roper and Zentall’s (1999) finding lies within the principles of conditioned reinforcement theory. Generally, this theory holds that the S+ stimulus reinforces observing responses through the associated secondary or conditioned reinforcement properties such as specific colours or shapes (Dinsmoor, 1983; Roper & Zentall, 1999). In particular, because the S+ stimulus is associated with primary reinforcement (e.g., food) more reliably or more immediately than unreliable signals, the presentation of the S+ stimulus effectively reinforces the behaviour that produces it (Roper & Zentall). Consequently, a discriminative stimulus that is always associated with 100% reinforcement become better conditioned reinforcers and are highly preferred, compared to unreliable signals, which are poorer conditioned reinforcers (Zentall & Stagner, 2012).

Thus, while Roper and Zentall’s (1999) finding may have been inconsistent with information theory – they are in fact, consistent with conditioned reinforcement theory. Specifically, their finding suggests that the pigeons highly preferred the conditioned reinforcer (S+ stimulus) associated with the discriminative alternative, compared to the unreliable stimuli that were associated with the non-discriminative alternative (Roper & Zentall, 1999). In addition, preference for this conditioned reinforcer appears to be strongest when the overall probability of reinforcement is quite low (Dinsmoor, 1983).

*Contrast.* In light of their findings, Roper and Zentall (1999) proffered that
positive contrast between the expected, and obtained reinforcement, provided a better explanation for their findings than information theory. In particular, they suggested that when the expected probability of reinforcement on the discriminative alternative was low (i.e., 12.5%), and reinforcement was obtained, the contrast between the expected and obtained reinforcement was large. For example, the expectation of reinforcement changed from 12.5% to 100% when reinforcement was obtained (an increase of 87.5% from expectation), despite the expectation of reinforcement being disconfirmed by the S- stimulus on 87.5% of those trials (Roper & Zentall, 1999). Thus, in this context, the S+ stimulus acquired additional value.

Alternatively, when the overall probability of reinforcement was high (i.e., 87.5%), the contrast between the expected and obtained reinforcement was small. For example, the expectation of reinforcement changed from 87.5% to 100% when reinforcement was obtained (an increase of 12.5% from expectation), even though that expectation was also disconfirmed by the S- stimulus on 12.5% of those trials (Roper & Zentall, 1999). In contrast, reinforcement was expected on the non-discriminative alternative 50% of the time, and the presentation of either stimulus associated with this alternative did not change that expectation (Roper & Zentall).

Consistent with this interpretation is the finding that discriminative stimuli can derive their saliency from Pavlovian conditioning (Jenkins, Barnes, & Barrera, 1981). For example, when a conditioned stimulus (e.g., S+) is presented infrequently in the context of a low-probability of reinforcement, the S+ results in a more rapid and reliable conditioning effect than if the conditioned stimulus occurred more frequently (Jenkins et al.; Stagner & Zentall, 2010; see also, Fantino, 2001; Grace & Hucks, 2013; Williams, 2002)

In support of the concept of positive contrast and conditioned reinforcement
theory, preference for a low-probability of reinforcement has only been found when discriminative stimuli differentially predict reinforcement (Gipson et al., 2009, Experiment 1; Roper & Zentall, 1999; Stagner & Zentall, 2010, Part A). When reinforcement is not differentially signalled, however, a strong preference for the alternative associated with unreliable stimuli and a higher probability of reinforcement has been reported (e.g., Fantino et al., 1979; Gipson et al., Experiment 2; Spetch et al., 1990; Stagner & Zentall, 2010; Part B; Zentall & Stagner, 2011a, Experiment 2) – a finding which is also consistent with optimal foraging theory (Stephens & Krebs, 1986). Interestingly, the results of earlier research involving discriminative stimuli and different probabilities of reinforcement have provided inconclusive evidence of the influence of information and conditioned reinforcement theory, and optimal foraging theory on choice behaviour. For example, when given a choice between an alternative that reliably predicted the presence (S+) and absence (S-) of 50% reinforcement, and another alternative that always signalled and provided 100% reinforcement (S+), some animals preferred the alternative associated with 50% reinforcement, while others preferred 100% (Belke & Spetch, 1994; Mazur, 1996; Spetch et al., 1990; Spetch et al., 1994).

It is unclear what theory (or combination of theories) are representative of these findings, or why there is much disparity between the results. For example, although both alternatives were associated with a strong conditioned reinforcer in Roper and Zentall’s (1999) study, all three theories would hold that the animal should opt for the 100% alternative; not only did it provide reliable information regarding reinforcement (i.e., S+), this alternative was also associated with a higher probability of reinforcement (i.e., 100%).
Alternatively, information and conditioned reinforcement theories would hold that the animal *should* opt for the 50% alternative (a notion which is inconsistent with optimal foraging theory). While this alternative provided a lower probability of reinforcement, it also provided reliable information with regard to the presence (S+) and absence (S-) of reinforcement, which were both equally likely. Perhaps, the results may have been more consistent if both alternatives had been associated with an overall lower probability of reinforcement (e.g., 12.5% reinforcement). If so, it is more than likely that there would be more consistency between the results, and conditioned reinforcement theory would have better explained their (hypothetical) findings (see Gipson et al., 2009).

*Delay Reduction Theory.* An alternative account of the saliency of discriminative stimuli and thus its strong preference, despite low-probabilities of reinforcement, is based on delay reduction theory (e.g., Fantino, 1969; Singer & Zentall, 2011). According to this theory, any stimulus that reliably predicts reinforcement in its presence than in its absence, can become a conditioned reinforcer if it is associated with a reduction in the delay to reinforcement (Fantino, 1969, 2001). Thus, a critical feature of delay reduction theory is the time between reinforcers associated with the S+ stimulus (Rachlin, 1990). For example, while most experiments usually hold equal, the absolute delay to reinforcement associated with the discriminative stimuli (S+ and S-), the relative delay to reinforcement generally is not (Singer & Zentall). On trials in which the S+ stimulus is consecutively presented and reinforcement is always obtained, the delay between reinforcers would be short, and the presentation of the S+ stimulus would not result in a large reduction in the delay to reinforcement. In contrast, if the S- stimulus was consecutively presented prior to the onset of the S+ stimulus, the delay between reinforcers would increase
until the S+ stimulus appeared and reinforcement was obtained. Thus, the appearance of the S+, in the context of an S- stimulus, would result in a large reduction in the delay to reinforcement and would therefore, acquire a better conditioning effect (Singer & Zentall; Zentall & Stagner, 2011b).

In contrast, unreliable stimuli associated with the non-discriminative alternative, does not reliably signal any reduction in delay to reinforcement, thus their signalling value is reduced. For example, the average wait for food on the non-discriminative alternative can be longer than it is on the discriminative alternative, and as a result, a strong preference for the alternative associated with discriminative stimuli should occur (e.g., see Mazur's modified hyperbolic-decay model which accounts for conditioned-reinforcement effects, Mazur, 1989; see also, Spetch et al., 1994).

Recently, Zentall and Stagner (2011b) assessed the value of reliable stimuli over unreliable stimuli by implementing a range of delays to reinforcement (Experiment 1). In their experiment, the discriminative alternative was associated with reliable stimuli, which reliably predicted the presence (S+) and absence (S-) of 20% reinforcement. In contrast, the non-discriminative alternative was associated with unreliable stimuli, which non-differentially signalled 50% reinforcement.

Using this arrangement, Zentall and Stagner (2011b) progressively reduced the delay to reinforcement associated with the non-discriminative alternative across delays of 10-, 8-, 6-, 4-, 2- and 0-s periods. The reduction in delay continued until the non-discriminative alternative was preferred over the discriminative alternative (which was held constant at 10-s). They then gradually increased the delay on the non-discriminative alternative until preference switched back to the discriminative alternative (Zentall & Stagner, 2011b, Experiment 1). They found that the delay to
reinforcement on the non-discriminative alternative had to be reduced from 10 s to 4.37 s before indifference was observed between the alternatives. This finding indicated that preference for reliable signals for reinforcement remained strong and were thus, highly valued despite manipulating the delays to reinforcement on the non-discriminative alternative (which had to be reduced by almost half before preference for this alternative developed; Zentall & Stagner, 2011b, Experiment 1).

To summarise, information, conditioned reinforcement, contrast and delay reduction theories place much value on discriminative stimuli that differentially predict reinforcement. This is supported by research which provides clear evidence that animals prefer stimuli that reliably predicts the presence (S+) and absence (S-) of reinforcement, compared to unreliable stimuli that do not. More importantly, they are willing to work hard and delay reinforcement to obtain those signals.

These theories and findings therefore support the fact that it is the signals (more specifically, the S+ stimulus), rather than the global amount of reinforcement (or reward) that is actually obtained, that may maintain gambling behaviour across species (Zentall, 2011; Zentall & Laude, 2013; Zentall & Stagner, 2011a). For example, just as wins are more salient to human gamblers (Breen & Zuckerman, 1999; Rachlin, 1990), so too is the S+ stimulus for animals. More recently, however, research has shown that like humans, who choose to forego money in their pocket for the low-probability of obtaining more by gambling, animals will choose to forego food for the low-probability of obtaining signals that reliably predict reinforcement (S+) and its absence (S-), even if the delivery of the primary reinforcer (e.g., food) is quite low. That is to say, like humans, animals gamble too.
Animal Models of Human Gambling

Early research findings indicated that under certain conditions, when given a choice between 50% or 100% reinforcement – each of which were associated with a strong S+ stimulus – some animals opted for 50% reinforcement while others did not (Belke & Spetch, 1994; Mazur, 1996; Spetch et al., 1990; Spetch et al., 1994). While there were inconsistencies between the results, this finding suggests that some animals would forego food to obtain discriminative stimuli that reliably predicted reinforcement (Gipson et al., 2009; Stagner et al., 2011; Stagner & Zentall, 2010). Such a suboptimal choice is analogous to a human gambler’s loss of ‘money’ in one’s pocket – but in this case, it is the non-human gambler’s loss of ‘food’.

To test the reliability and robustness of this finding, Gipson et al. (2009) proposed that if they reduced the probability of reinforcement associated with the non-discriminative alternative, they may find more consistent results (Experiment 2). In particular, they sought to find a statistically reliable preference for the discriminative stimuli associated with a lower probability of reinforcement, over unreliable stimuli associated with a higher probability of reinforcement (Gipson et al.).

Using a procedure similar to that of Roper and Zentall (1999), Gipson et al. (2009) presented pigeons with a choice between two alternatives (Experiment 2). Choice of the discriminative alternative provided stimuli that reliably predicted the presence (S+) and absence (S-) of a low-probability of 50% reinforcement. In contrast, choice of the non-discriminative alternative provided one of two unreliable stimuli, each of which non-differentially signalled a higher probability of 75% reinforcement, regardless of the stimulus presented (Gipson et al.).

In their design, pigeons were simultaneously presented with these options on
two white side keys (i.e., initial-links) during choice trials (Gipson et al., 2009, Experiment 2). A single response on either key fulfilled the initial-link response requirement (FR 1) and initiated the terminal-link stimuli and its associated outcome on the chosen key. This was signalled by the immediate presentation of one of two coloured stimuli (e.g., S1 or S2, and S3 or S4) for a fixed duration of 30-s (FT 30-s). Each stimulus occurred with a probability of .50 on each alternative. If the stimulus was associated with the discriminative alternative, the presentation of S1 always resulted in reinforcement (S+), while S2 did not (S-). This meant that on half of the trials, S1 provided 100% reinforcement and on the remaining trials, S2 provided 0% reinforcement, even though choice of this alternative provided 50% reinforcement overall (Gipson et al.).

Alternatively, if the stimulus was associated with the non-discriminative alternative, the presentation of S3 or S4, non-differentially signalled reinforcement 75% of the time the stimulus was presented. Under this arrangement, while choice of this option provided unreliable stimuli, the probability of reinforcement associated with the non-discriminative alternative was higher (75%) than the discriminative alternative (50%) which provided reliable stimuli (Gipson et al., 2009). To ensure the pigeons had adequate experience with the reinforcement contingencies associated with each alternative, the pigeons received 48 forced-choice trials (24 forced trials to the left-key, and 24 to the right) which were randomly interspersed with 12 choice trials.

In support of their hypothesis, Gipson et al. (2009) found a statistically reliable, but suboptimal preference of 69%, for the discriminative stimuli associated with the low-probability of 50% reinforcement. Thus, their findings provided strong evidence that animals prefer signals that reliably predict reinforcement and its
absence, and more importantly, they were willing to forego food to obtain those signals. The results of Gipson et al.’s study also suggested that the value of the discriminative stimuli outweighed the global amount of reinforcement that could have been obtained. For example, had the pigeons chosen optimally and selected the non-discriminative alternative associated with unreliable stimuli, they could have obtained 50% more food (Gipson et al.). Their finding also supports the speculation that had earlier research reduced the alternative associated with the higher probability of reinforcement, those findings might have been more consistent and therefore reliable (see Gipson et al., cf., Belke & Spetch, 1994; Mazur, 1996; Spetch et al., 1990; Spetch et al., 1994).

In a follow-up study, Stagner and Zentall (2010) proposed that if they further reduced the overall probability of reinforcement associated with the discriminative alternative to 20%, a larger preference for this alternative might be obtained. Using a procedure similar to that of Gipson et al. (2009, Experiment 2), Stagner and Zentall (2010) gave pigeons a choice between two alternatives. Choice of the discriminative alternative provided stimuli that reliably predicted the presence (S+) and absence (S-) of 20% reinforcement. In contrast, choice of the non-discriminative alternative provided unreliable stimuli that non-differentially signalled 50% reinforcement, regardless of the stimulus presented. For convenience, an illustration of their general design (and the design used in this experiment) is presented in Figure 1.

Both options were presented on two white side keys (i.e., initial-links) during choice trials. An FR 1 on either key fulfilled the initial-link response requirement, and initiated the terminal-link stimuli and its associated outcome on the chosen key. This was signalled by the immediate presentation of one of two coloured stimuli for a FT 10-s. Unlike Gipson et al. (2009, Experiment 2), however, each stimulus within
Figure 1. General procedure used in this experiment (Stagner & Zentall, 2010). Hens chose between two alternatives during choice-trials. Choice of the low-probability alternative provided stimuli that reliably predicted 100% reinforcement on 20% of the trials, and 0% reinforcement on the remaining 80% of trials. In contrast, choice of the non-discriminative alternative provided one of two unreliable stimuli that non-differentially signalled 50% reinforcement, regardless of the stimulus presented. Adapted from “Suboptimal Choice Behavior by Pigeons” by J. P. Stagner and T. R. Zentall, 2010, Psychonomic Bulletin & Review, 17(3), 412-416. Copyright 2010 by The Psychonomic Society, Inc. Reprinted with permission.
each pair in Stagner and Zentall's (2010) study, occurred with a probability of .20 and .80, respectively, on each alternative. This meant, for example, S1 was presented on 20% of the trials while S2 was presented on the remaining 80% of the trials for this key, and the outcome associated with each stimulus, was provided following its FT 10-s presentation.

If the stimulus was associated with the discriminative alternative, the presentation of S1 always resulted in reinforcement (S+) while S2 did not (S-). For example, on 20% of the trials, S1 provided 100% reinforcement; on the remaining 80% of the trials for this alternative, S2 provided 0% reinforcement. Thus, choice of this option therefore provided a low-probability of 20% reinforcement (Stagner & Zentall, 2010).

If the stimulus was associated with the non-discriminative alternative, the presentation of S3 or S4 non-differentially signalled 50% reinforcement, regardless of the stimulus presented. Under this arrangement, while choice of this option provided unreliable stimuli, the probability of reinforcement associated with the non-discriminative alternative was higher (50%) than the discriminative alternative (20%) which provided reliable stimuli (Stagner & Zentall, 2010).

Like Gipson et al. (2009), Stagner and Zentall (2010) ensured the pigeons had adequate experience with the reinforcement contingencies associated with each alternative by randomly interspersing 40 forced-choice trials (20 forced trials to the left-key, and 20 to the right) with 20 choice trials. Using this design, Stagner and Zentall found a greater suboptimal preference of 97%, for the discriminative stimuli associated with a low-probability of 20% reinforcement, compared to Gipson et al.’s finding of a 69% preference, for a low-probability of 50% reinforcement. The
consequence of this suboptimal choice meant that the pigeons in Stagner and Zentall’s study lost 60% of food that could have been obtained had they chosen optimally, and selected the non-discriminative alternative associated with 50% reinforcement.

Figure 2 presents the results of Stagner and Zentall’s study (see in particular, Phase 1 in Figure 2, for the results for this phase of their study).

In addition, when the stimuli and reinforcement contingencies associated with the side keys were reversed in Phase 2 of their study, Stagner and Zentall (2010) found that preference for the discriminative alternative quickly reversed as well (see Phase 2 in Figure 2). To determine whether pigeons would follow other discriminative stimuli at the time of choice, in Phase 3 of their study, Stagner and Zentall used shapes (i.e., a circle and a plus sign), as opposed to white initial-link keys, to signal each alternative. In addition, the shapes randomly moved between the side keys from trial to trial. A response made to either shape, led to its associated alternative and terminal-link stimuli (i.e., red, green, blue or yellow colours), and its corresponding outcome (i.e., food or no food). Results showed that the pigeons followed the shape that was associated with the discriminative stimuli and the low-probability of 20% reinforcement (see Phase 3 in Figure 2).

An interesting aspect of their study, was their last phase (Phase 4) which assessed the role of discriminative stimuli and the strong preference they found for the low probability of reinforcement (Stagner & Zentall, 2010). In this phase, each stimulus within each alternative retained its probability of occurrence (i.e., .20 and .80, respectively), but the probability of reinforcement associated with the discriminative stimuli, was equated at 20%. This meant that the S+ stimulus that was presented on 20% of the trials, and originally associated with 100% reinforcement
Figure 2. Results of Stagner and Zentall’s (2010) study showing preference for stimuli that differentially predicted a low-probability of 20% reinforcement, over unreliable stimuli that non-differentially signalled a higher probability of 50% reinforcement (Phase 1, Training); reversal of the stimuli and reinforcement contingencies associated with the side keys (Phase 2, Reversal); training with discriminative shape stimuli that signalled each alternative, and moved between the side keys from trial to trial (Phase 3, Discrimination); removal of the predictive reliability of the stimuli associated with the low-probability alternative (Phase 4, No Differential Conditioned Reinforcement). Adapted from “Suboptimal Choice Behavior by Pigeons” by J. P. Stagner and T. R. Zentall, 2010, *Psychonomic Bulletin & Review*, 17(3), 412-416. Copyright 2010 by The Psychonomic Society, Inc. Reprinted with permission.
every time it was presented, was reduced from 100% reinforcement to 20%.

Similarly, the S- stimulus which was presented on the remaining 80% of the trials on this alternative, and originally associated with 0% reinforcement every time it was presented, was raised from 0% reinforcement to 20% (Stagner & Zentall). While this arrangement left the overall probability of reinforcement associated with the two alternatives the same (i.e., 20% vs., 50% reinforcement), it effectively made the reliability of the discriminative stimuli on the low-probability alternative, unreliable.

When the reliability of the discriminative stimuli was removed, in keeping with optimal foraging theory (Stephens & Krebs, 1986), a strong optimal preference of 87.8% was found for the higher probability of 50% reinforcement (Stagner & Zentall, 2010; see Phase 4 in Figure 1). The findings from Stagner and Zentall’s (2010) study are provocative, because they revealed an even stronger suboptimal preference for discriminative stimuli associated with an overall, lower probability of reinforcement than has previously been found (cf., Gipson et al., 2009; Roper & Zentall, 1999). Their results also compliment Gipson et al.’s (2009) finding that animals are willing to forego a vast amount of food (e.g., 60% loss of food) to obtain signals that reliably predict the presence (S+) and absence (S-) of a low-probability of reinforcement. What is not clear, however, is what mechanism is responsible for this suboptimal choice. Nor is it clear, what theory – or combination of theories (i.e., information, conditioned reinforcement, contrast and delay reduction theories) – are representative of this finding.

**Accounting for Suboptimal Choice: Positive Contrast, Certainty of Reinforcement, Ambiguity-Aversion, or Conditioned Reinforcement and Observing Behaviour?**

*Positive Contrast.* Consistent with Roper and Zentall’s (1999) account of
suboptimal choice, both Gipson et al. (2009) and Stagner and Zentall (2010) proffered that the mechanism responsible for the suboptimal preference found in their studies, was positive contrast. In particular, the researchers proposed that it was the positive contrast between the probability of reinforcement associated with the discriminative alternative at the time of choice, and the onset of the S+ stimulus prior to reinforcement, which gave the S+ stimulus added value. Thus, in the case of Gipson et al., a suboptimal choice of the discriminative alternative meant that 50% reinforcement would have been expected at the time of choice, but the appearance of the S+ stimulus, signalled 100% reinforcement, resulting in a 50% increase from expectation. Similarly, a suboptimal choice of the discriminative alternative in Stagner and Zentall’s study meant that 20% reinforcement would have been expected at the time of choice, but the appearance of the S+ stimulus once again signalled 100% reinforcement, which resulted in an 80% increase from expectation. Of note, however, is that the expectation of reinforcement in both studies, was also disconfirmed by the S- stimulus on 50% (Gipson et al.) and 80% (Stagner & Zentall) of those trials.

In contrast, an optimal choice of the non-discriminative alternative meant that 75% (Gipson et al., 2009) and 50% (Stagner & Zentall, 2010) reinforcement would have been expected at the time of choice, but the appearance of either stimulus associated with this option, did not change that expectation. Thus, the results of these studies (Gipson et al.; Stagner & Zentall), suggest that the appearance of the discriminative stimuli enhanced the value of the alternative that they were associated with, even though that alternative was also associated with a lower probability of reinforcement.
Certainty of Reinforcement. An alternative but related mechanism proposed by Zentall and Stagner (2011a, 2011b), was that suboptimal choice resulted from the certainty of reinforcement associated with the S+ stimulus as it reliably predicted reinforcement every time it was presented. Whilst this proposition is reminiscent of information theory, the procedure used to test this speculation would not support an information theoretical account of any results obtained. This is because Zentall and Stagner (2011b) used a procedure similar to that of Stagner and Zentall (2010) in which the presence and absence of reinforcement were not equally likely, and the probability of reinforcement was low. In particular, Zentall and Stagner decreased the probability of reinforcement associated with the S+ stimulus from 100% to 80%, such that the overall probability of reinforcement associated with the low-probability alternative, was reduced from 20% reinforcement to 16% (Experiment 2). Under this arrangement, reinforcement was no longer certain on this alternative. Similarly, the probability of reinforcement associated with the non-discriminative alternative, was also reduced from 50% reinforcement to 40%.

Using this design, they found that the results did not support their certainty of reinforcement hypothesis. This was because a strong suboptimal preference of 91.2% was still obtained for the discriminative stimuli associated with the low-probability of 16% reinforcement (Zentall & Stagner, 2011b). Although it was noted by the researchers that choice for this alternative took longer to develop under these conditions, it appeared that the uncertainty of the S+ stimulus that preceded reinforcement on the low-probability alternative, did not deter the pigeon’s suboptimal choice for this option (Zentall & Stagner).

Consequently, an information theoretical account of their finding would not
hold because, according to this theory, when the probability of reinforcement is low, a *weaker* preference for the discriminative alternative should have been found. This is because the expectation of 16% reinforcement was unlikely on this alternative, and was generally not obtained (Roper & Zentall, 1999; Stagner & Zentall, 2010; Zentall, 2011). But this was not the case.

*Ambiguity-Aversion.* Alternatively, Zentall and Stagner (2011a) proposed that the findings of earlier research might not have resulted from the certainty of reinforcement associated with the S+ stimulus, but from an aversion to the ambiguity of the outcome associated with the non-discriminative alternative. For example, they suggested that although choice of the non-discriminative alternative provided a higher probability of reinforcement, the stimuli that signalled reinforcement on this alternative were ambiguous and thus, reinforcement was uncertain. In contrast, choice of the discriminative alternative provided reliable stimuli that differentially predicted the presence (S+) and absence (S-) of the lower probability of reinforcement. This arrangement meant that the reliability of the stimuli on the discriminative alternative removed all ambiguity associated with this option, therefore, reinforcement was certain, even when the S- stimulus signalled no reinforcement (Zentall & Stagner).

To test this ambiguity-aversion hypothesis, Zentall and Stagner (2011a) used a procedure similar to that of Stagner and Zentall (2010), but instead of manipulating the probability of reinforcement associated with each alternative, they manipulated the magnitude of reinforcement. This procedural design provides an interesting simulation of human gambling behaviour because “when humans gamble, the alternatives generally involve different magnitudes of reinforcement (typically
money) rather than different probabilities of reinforcement” (Zentall, 2011, p.53). In
addition, it was further speculated that if the suboptimal choice found in previous
studies (e.g., Gipson et al., 2009; Stagner & Zentall, 2010) was a good analogue of
human gambling behaviour, then a similar preference should be found using the
present design (Zentall & Stagner).

In their experiment, choice of the discriminative alternative provided a
stimulus that on 20% of the trials, reliably predicted 10 pellets of food (Zentall &
Stagner, 2011a, Experiment 1). On the remaining 80% of the trials with this
alternative, another stimulus reliably predicted zero pellets of food. This alternative
was therefore associated with a low-probability of 20% reinforcement. In contrast,
choice of the non-discriminative alternative was associated with 50% reinforcement.
In this alternative, one of two stimuli were presented, each of which delivered 3
pellets of food on every trial. Thus, the uncertainty of the outcome associated with
the non-discriminative option was therefore removed (Zentall & Stagner, Experiment
1).

This design generally meant that there was no ambiguity of reinforcement
associated with any stimulus used in their experiment. This is because choice of the
discriminative alternative was associated with an average of 2 pellets of food per trial,
whereas the non-discriminative alternative was always associated with a certain 3
pellets of food (Zentall & Stagner, 2011a). A further speculation was if pigeons were
sensitive to the relative amounts of food that could be obtained from each alternative,
it was thought that under this arrangement, the pigeons would choose the optimal,
non-discriminative alternative which was associated with a higher probability of
reinforcement (i.e., 3 pellets of food).
In spite of this design, however, Zentall and Stagner (2011a) found a strong suboptimal preference of 82.2%, for the discriminative stimuli associated with the low-probability alternative of 20% reinforcement (Experiment 1). This finding suggested that the suboptimal choice found in earlier studies was not caused by the ambiguity of the outcomes associated with the non-discriminative alternative. This is because, when the ambiguity of this alternative was removed, suboptimal choice for the discriminative stimuli still occurred (Zentall & Stagner, Experiment 1), therefore, the pigeons were insensitive to the relative amounts of food that was obtainable.

In addition, Zentall and Stagner (2011a) demonstrated that this preference did not result from the variability of reinforcement associated with the discriminative alternative (10 or zero pellets of food). This was confirmed in Experiment 2 of their study where they equated the probability of reinforcement associated with each discriminative stimulus, at 20%. That is, on 20% of the trials, both low-probability stimuli provided 10 pellets of food, and on the remaining 80% of the trials, both stimuli provided zero pellets. This arrangement effectively made the reliability of the stimuli on the low-probability alternative, unreliable.

Using this design, Zentall and Stagner (2011a) found a strong *optimal* preference of 79.9%, for the higher probability of 50% reinforcement (Experiment 2) – a finding which is consistent with optimal foraging theory (Stephens & Krebs, 1986). The researchers proposed that the results obtained in Experiment 2 of their study suggested that the suboptimal preference found in Experiment 1, was due to the signalling value of the discriminative stimuli. For example, they proposed that the reliability of the stimuli in terms of differentially predicting the presence (S+) and absence (S-) of 10 pellets of food in Experiment 1, gave the discriminative stimuli
added value – thus, the stimuli were highly valued in this context (Zentall & Stagner, 2011a). In contrast, the signalling value of the discriminative stimuli diminished in Experiment 2 because the stimuli were now unreliable predictors of 20% reinforcement. As a result, the stimuli were attributed negative value in this context and consequently, the pigeons became sensitive to the relative amounts of food that could be obtained from the alternatives.

*Conditioned Reinforcement and Observing Behaviour.* Another possibility was proposed by Dinsmoor (1983), who suggested that a combination of conditioned reinforcement and observing behaviour was responsible for the suboptimal preference found, in the research outlined above. In particular, he believed that any S+ stimulus that reliably predicted reinforcement with a high probability (e.g., 100% reinforcement), would become a conditioned reinforcer and thus, elicit observing behaviour (Dinsmoor; see also, Gipson et al., 2009; Zentall, 2011). Clearly, any stimulus that reliably predicted 100% reinforcement would be preferred over other stimuli that signalled a lower occurrence of reinforcement (e.g., 50% reinforcement, Stagner & Zentall, 2010; 75% reinforcement, Gipson et al.; or even 0% reinforcement as reliably predicted by the S- stimulus on the discriminative alternative).

If this speculation is correct, and these mechanisms are responsible for suboptimal choice, it is unclear why this preference is not tempered by the conditioned inhibition of the S- stimulus which reliably predicts the absence of reinforcement (Gipson et al., 2009; Zentall, 2011). Especially since the S- stimulus occurred four times more often in some experiments than the S+ stimulus (e.g., Stagner & Zentall, 2010; Zentall & Stagner, 2011a). For example, the high occurrence of the S- stimulus should have reduced the attractiveness of the S+
stimulus and thus, a decline in preference for this option should have been observed (Gipson et al.) – a speculation which is consistent with an information theoretical account of suboptimal choice. As demonstrated by the results, however, choice for this alternative did not decrease which suggests that conditioned reinforcement theory, by itself, may not provide an adequate account of suboptimal choice (see Stagner et al., 2012).

Alternatively, it has been suggested that the S- stimulus might fail to induce conditioned inhibition because once it was identified as the S-, the pigeons turned away from it. As a result, any inhibitory effect would be reduced as the S- stimulus would maintain little observing behaviour (see Dinsmoor, 1983; Gipson et al., 2009; Stagner et al., 2011).

Consistent with this speculation is that many studies found that the pigeons rarely pecked at the S- stimulus, whereas they consistently pecked at all the stimuli associated with reinforcement (e.g., Gipson et al., 2009; Stagner & Zentall, 2010; Zentall & Stagner, 2011a). In contrast, Dinsmoor found that when pigeons were able to turn off the S- stimulus (which had no effect on the schedule of reinforcement in effect), they did so (see Dinsmoor, 1983). His results thus demonstrated that the S-stimulus does acquire some inhibitory properties (Dinsmoor).

Recently, however, Stagner et al. (2011) compared the results of three different groups of pigeons which were either assigned to a condition in which a ceiling mounted house-light signalled the presence (S+) of reinforcement, or its absence (S-), and another condition in which no house-light was used (i.e., Stagner and Zentall’s, 2010, results were analysed). This design effectively made the S-stimulus more salient and less avoidable. Under this arrangement, Stagner et al.,
(2011) found a consistently strong suboptimal preference for the discriminative stimuli associated with the low-probability of reinforcement, for each group (i.e., S+ = 97.1%, S- = 92.5%, no house-light = 97.5%). These results suggest that little negative value was attributed to the S- stimulus because its saliency did not deter the pigeons from choosing suboptimally. They also provide further support to Breen and Zuckerman’s (1999) proposition that wins (in this case, the S+ stimulus) are more salient to gamblers, than their more frequent losses (in this case, the occurrence of the S- stimulus). Thus, it appears that once again, preference for discriminative stimuli was more valued than the amount of reinforcement that was obtainable from each alternative.

To summarise, it has been proposed that positive contrast, certainty of reinforcement, ambiguity-aversion, and conditioned reinforcement together with observing behaviour, are mechanisms that may be responsible for suboptimal choice behaviour. Each mechanism places much value on the discriminative stimuli associated with the low-probability of reinforcement, or the ambiguous nature of the non-discriminative alternative. Research showed, however, that any manipulation made to make the S+ and S- stimuli or the unreliable stimuli on the non-discriminative alternative, more or less salient or certain, did not deter the pigeons from choosing suboptimally. That is of course, with the exception of making the reliability of the low-probability stimuli, unreliable (e.g., Zentall & Stagner, 2011a, Experiment 2; see also, Stagner & Zentall, 2010, Part B).

Collectively, the research outlined above provides strong evidence that it is the value of the discriminative stimuli that outweighed the global amount of reinforcement that could have been obtained. This is evidenced by their subject’s
consistent choice to forego a substantial loss of food, for the low-probability of obtaining reliable signals that differentially predicted reinforcement. Thus, it appears that under these conditions, the animals simulated human gambling behaviour. Of particular interest to the present study is if animals prefer reliable signals that differentially predict reinforcement, regardless of the consequences that are associated with those signals, how unreliable must those signals be, before animals begin choosing optimally?

The Experiment: An Investigation of Suboptimal Choice Behaviour

The purpose of this experiment was to determine whether animals exclusively choose signals that reliably signal a reinforcing outcome irrespective of the consequences that are associated with those signals. Of particular interest, however, was the signalling value of the discriminative stimuli associated with the low-probability alternative, and how choice for this option could be affected when the reliability of those signals become less reliable.

Using Stagner and Zentall’s (2010) procedure, the present experiment partially replicated Phases 1, 2 and 4 of their study, to assess the reliability and robustness of their findings. Their procedure was employed because Stagner and Zentall reported a stronger suboptimal preference for discriminative stimuli associated with a lower probability of reinforcement, than has previously been found (cf., Gipson et al., 2009).

In this experiment, choice of the low-probability alternative generally provided stimuli that reliably predicted the presence (S+) and absence (S-) of 20% reinforcement. In contrast, choice of the non-discriminative alternative provided unreliable stimuli that non-differentially signalled 50% reinforcement, regardless of
the stimulus presented.

It should be noted that the design of this experiment departs from Stagner and Zentall’s (2010) procedure in three important ways. First, to test the generality of their findings across species, hens were used instead of pigeons. Another procedural artefact is that shapes were not employed in this experiment, nor did the stimuli move between the keys during this series of conditions (i.e., Conditions 7-11). Finally, a condition was implemented during the replication series of conditions (Conditions 1-4, and Condition 6), where the occurrence of each stimulus, and their corresponding probability of reinforcement, were equated at 50% (i.e., Condition 5).

Of particular note is that all of the research on suboptimal choice thus far, has pooled data over a series of sessions, and reported group mean choice proportions to each alternative’s initial-link key. An unintentional artefact of this technique is that it potentially masks individual differences. As a result, group means can be skewed due to unintended ceiling or floor effects, and the effects of manipulating the reinforcement contingencies associated with each alternative, can be obscured (Roper & Zentall, 1999; Zentall & Singer, 2007). In light of this potential, each hen’s data from each condition is reported. With the exception of the departures previously outlined, the present experiment comprised three series of conditions. They included a replication series (Conditions 1-6), a reliability of stimuli series (Conditions 7-11), and a controls for bias series (Conditions 12 and 13).

Replication Series (Conditions 1-6). This series of conditions partially replicated Phases 1 and 2 of Stagner and Zentall’s (2010) procedures. In Phase 1 of their study, Stagner and Zentall (2010) found a strong suboptimal preference of 97%, for the discriminative stimuli associated with a low-probability of 20%
reinforcement. In addition, when they reversed the stimuli and reinforcement contingencies associated with the side keys in Phase 2 of their study, they found that preference for the discriminative stimuli quickly reversed as well.

In this experiment, the paired stimuli and reinforcement contingencies associated with the side keys were continually reversed across Conditions 1-4 and Condition 6. This arrangement meant that the reliability and robustness of Stagner and Zentall’s (2010) findings in Phases 1 and 2 of their study, could be thoroughly investigated. It was hypothesised that the hens would demonstrate a strong suboptimal preference for the discriminative stimuli associated with the low-probability of 20% reinforcement. It was also hypothesised that when the stimuli and reinforcement contingencies associated with the side keys were reversed, choice for the discriminative stimuli would quickly reverse as well.

In Condition 5, however, the occurrence of each stimulus and its corresponding probability of reinforcement, were equated at 50%. This condition was implemented to assess choice performances between the side keys when reliable signals for reinforcement were withheld, and reinforcement was equally likely. It was hypothesised that the hens would demonstrate indifference between the alternatives in this condition.

**Reliability of Stimuli Series (Conditions 7-11).** The aim of this series of conditions was to partially replicate Phase 4 of Stagner and Zentall’s (2010) procedure, and extend their findings. Of particular interest was their finding that when the reliability of the discriminative stimuli were made unreliable in Phase 4 of their study, a relatively strong preference for the higher probability of 50% reinforcement was found (see also, Zentall & Stagner, 2011a, Experiment 2). In light
of this finding, the purpose of Conditions 7-11 was to determine the point at which
the subjects would choose the non-discriminative alternative over the low-probability
alternative when the reliability of the stimuli that differentially predicted 20% 
reinforcement, was gradually made less reliable over a series of conditions. It was
hypothesised that a strong preference for the non-discriminative alternative would be
observed for all hens if the slightest manipulation were made, to make the reliability
of the low-probability stimuli less reliable.

 Controls for Bias Series (Conditions 12 and 13). The aim of this series of
conditions was to rule out, side and colour biases by reversing two conditions used in
the previous series of conditions. This arrangement therefore, was a partial
combination of Phases 2 and 4 of Stagner and Zentall’s (2010) procedure.

Another aim of this series of conditions was to investigate the presence of
hysteresis in the data. Because performance in subsequent conditions can be
influenced by the contingencies experienced in previous conditions, it was thought
that the presence of hysteresis would provide an alternative measure of each subject’s
preference for reliable signals for reinforcement, rather than the reinforcement
contingencies associated with each alternative (Davidson & Baum, 2000). Thus, a
short transitional period of hysteresis would suggest a strong preference for this
alternative while longer transitional periods would suggest a weaker preference for
this option. It was hypothesised that a strong suboptimal preference for the stimuli
associated with the low-probability alternative of 20% reinforcement would be
observed in Condition 12. It was also expected that a short transitional period of
hysteresis would be observed in the data, indicating a strong preference for this
option.
In contrast, it was hypothesised that all hens would exhibit an optimal preference for the unreliable stimuli associated with a higher probability of 50% reinforcement in Condition 13, and that a short transitional period of hysteresis would be observed in this condition as well. This is because choice for the low-probability alternative was expected to rapidly decrease, and preference for the non-discriminative alternative would stabilise relatively quickly.
Method

Subjects

The subjects were six Brown-Shaver domestic hens, numbered 12.1 through 12.6. All hens were approximately two years old at the beginning of the experiment, and had previous experience responding on simple schedules of reinforcement. The hens were housed individually in home cages (500-mm long x 450-mm wide x 450-mm high), in a ventilated colony room which was maintained on a 12-hr light: 12-hr dark cycle. While in their home cages, the hens were provided with free access to water, ad libitum, with weekly provisions of grit and vitamin supplements. All hens exhibited red fleshy combs throughout this experiment, which suggests good health.

Hen Weights. All hens were weighed daily. Prior to starting experimental sessions, the hens were given free access to commercial layer pellets for 45 days to stabilise their weights. Towards the end of this period, an average free-feeding weight range (+/- 2 gms) was calculated over 15 days for each hen. The average running weight percentages for each hen was between 81.1% and 87.2% of their free-feeding body weight. Table 1 shows each hen’s free-feeding and running weights averages, with standard deviations. Weight range maintenance was assisted by supplementary post-session feeding of commercial layer pellets if necessary.

Experimental sessions ran seven days a week and began at approximately 9.00 am each day. Consent was obtained from the University of Waikato’s Animal Ethics Committee, so that the hens could take part in this study (protocol number: 870), and all hens were cared for in accordance with the University of Waikato’s animal care guidelines.
Table 1. *Free-feeding and running weight averages (+/- 2gms), for each hen, including average free-feeding weight percentages, and standard deviations (in parentheses).*

<table>
<thead>
<tr>
<th>Hen</th>
<th>12.1</th>
<th>12.2</th>
<th>12.3</th>
<th>12.4</th>
<th>12.5</th>
<th>12.6</th>
</tr>
</thead>
<tbody>
<tr>
<td>Average Free-feeding Weight (+/- 2gms)</td>
<td>1944</td>
<td>2370</td>
<td>1994</td>
<td>2240</td>
<td>2030</td>
<td>2156</td>
</tr>
<tr>
<td>Average Running Weight</td>
<td>1576</td>
<td>2027</td>
<td>1710</td>
<td>1907</td>
<td>1771</td>
<td>1825</td>
</tr>
<tr>
<td>Average Percentage of Free-feeding Weight</td>
<td>81.1% (4.0)</td>
<td>85.5% (2.0)</td>
<td>85.7% (2.0)</td>
<td>85.1% (2.2)</td>
<td>87.2% (2.9)</td>
<td>84.6% (2.2)</td>
</tr>
</tbody>
</table>

**Apparatus**

The apparatus was a particleboard experimental chamber (575-mm long x 430-mm wide x 540-mm high), located in a room with several other experimental chambers. The interior surfaces were painted white, and the chamber floor was covered with a thin removable rubber doormat (560-mm long x 390-mm wide).

The chamber was equipped with three circular response keys and a food hopper that were located on one wall of the chamber. The response keys were made of semi-translucent Perspex, and were horizontally aligned 400-mm above the chamber floor. Each response key was 30-mm in diameter and 100-mm apart, center to center. The response keys could be trans-illuminated from the rear using a 28-V multi-chip LED (light-emitting diode) bulb which illumined white (unfiltered), red (637 nms), green (526 nms), blue (470 nms), and yellow (590 nms). Surrounding each response key was an aluminium plate (110-mm long x 50-mm wide) that was spaced 50-mm apart, plate to plate. The distance between the top of the keys to the top of the plates was 45-mm, and from the bottom of the keys to the bottom of the
plates was 35-mm. The distance between the top of the plates to the top of the chamber was 55-mm, and from the bottom of the plates to the chamber floor was 365-mm.

An effective response on each key required a force of not less than 0.2 N (20-g), which resulted in a brief audible feedback beep. No feedback or consequences were scheduled for responses made to unlit keys.

A food hopper, which provided access to wheat when the hopper was raised, was situated 180-mm below the response keys. The food hopper was mounted behind a rectangular opening (100-mm high x 70-mm wide) that was centred 120-mm above the chamber floor. When operational, the food hopper was illuminated by a white LED bulb (situated 35-mm above the hopper), and the hopper was raised. An infra-red beam, connected inside the food hopper, ensured each hen gained 2-s access to wheat, from the time the hen put its head into the hopper. During reinforcement periods, all key lights were extinguished, and any responses made to extinguished keys were ineffective. If after 3 s, reinforcement was not obtained, the food hopper was lowered and the next trial began. The light emitted from the response keys and the food hopper were the only sources of illumination in the experimental chamber.

Experimental events were controlled and recorded by a Dell PC computer running Med-PC® IV software which was located in the same room as the experimental chamber, and a summary of the data was manually logged into a data book at the end of each session.

Procedure

Experimental sessions were conducted daily. Each hen was removed from her home cage, weighed, placed into the experimental chamber, and the programme was
started by the experimenter. Data was discarded from all experimental sessions if fewer than 12 trials had been completed, or an egg had been laid in the chamber during a session.

Pre-training Phases. All hens were exposed to two initial pre-training phases; a Continuous Schedule of Reinforcement (CRF) phase, and a Fixed-Interval 10-s (FI 10-s) phase. Each phase included 48 stimulus presentations (white, red, green, blue and yellow colours) per session: Four involving each of the five colours on the left and right side keys, with two additional presentations of white on the center-key (in addition to its presentations on the side keys). A 10-s Intertrial Interval (ITI) separated each trial in each phase.

During the CRF phase, all hens were trained to peck each coloured stimulus for reinforcement. Each stimulus was randomly presented across the response keys, and a single peck made to an illuminated response key, resulted in 2-s access to wheat. All hens received two CRF pre-training sessions except Hen 12.1, who received five sessions.

All hens were then trained to peck each of the five coloured stimuli which were randomly presented across the response keys on a FI 10-s schedule of reinforcement without replacement (the first response after 10-s had elapsed was reinforced with 2-s access to wheat). All hens received four FI 10-s pre-training sessions except Hen 12.1, who required an additional seven FI 10-s sessions (11 in total) before she was consistently responding to each stimulus on each key.

Following the completion of this pre-training regime, all hens were introduced to the first experimental condition described further below.
**General Procedure**

The general design of this experiment is presented in Figure 1. The presentation of each stimulus and the delivery of reinforcement were provided using different probabilities for each event in this experiment. The contingencies for each event were delivered using a chained procedure which resulted in one of two alternative schedules – either a low-probability alternative associated with stimuli that reliably predicted 20% reinforcement, or a higher non-discriminative alternative associated with unreliable stimuli that non-differentially signalled 50% reinforcement.

Each chained schedule was associated with the left- or right-side key. Access to each alternative and its associated reinforcement contingencies was provided via a response made in the presence of a white-side key (initial-link). This response completed the Fixed-Ratio 1 (FR 1) initial-link requirement, and resulted in the immediate illumination of a coloured stimulus (terminal-link) for 10 s, which was associated with the alternative in effect on the particular key. After 10 s, the terminal-link provided an outcome, either 2-s access to wheat, or a 3-s blackout period, independent of a response.

**Pairing of Stimuli.** Both side keys could be lit with each discriminative stimulus (white, red, green, blue, and yellow). For the duration of this experiment, each stimulus (except white) was paired with another stimulus (e.g., red and green, Rd/Gn, and blue and yellow, Bl/Ye). The paired colours formed the terminal-link stimuli that were associated with each alternative and its corresponding reinforcement contingencies. Each pair was presented on the left- or right-side key in a condition. The presentation of white on the center-key, signalled the start of each trial; and when presented on the side keys, white signalled the initial-link that led to the
corresponding terminal-link stimuli and its associated reinforcement contingencies on that key.

**Presentation Probabilities of Stimuli.** Each stimulus within each pair, was presented with a constant probability of .20 and .80, respectively. When illumined, each coloured stimulus was presented for a fixed duration of 10-s (FT 10-s). For example, Rd was presented on the left-key for 20% of the trials, with presentations of Gn on the remaining 80% of the trials for that key, and each stimulus was presented for a FT 10-s. Similarly, if Bl/Ye were associated with the right-key, each stimulus had a presentation probability of .20 and .80, respectively. Thus, Bl was presented on the right-key for 20% of the trials, while Ye was presented on the remaining 80% of the trials for that key, and each coloured stimulus was presented for a FT 10-s.

**Probabilities of Reinforcement.** In addition to each stimuli’s differential presentation probability, each stimulus within each pair was also associated with a different probability of reinforcement ($P(\text{rf})$) for each condition. Reinforcement probabilities ranged from 0.0, .50, and 1.0. As a continuation of the previous example, if Rd/Gn was also associated with a $P(\text{rf})$ 1.0 and 0.0 (100% and 0% reinforcement for each stimulus) contemporaneously with a presentation probability of .20 and .80, respectively, this meant that on 20% of the trials on the left-key, Rd was presented and after 10 s, reinforcement was always provided (S+). On the remaining 80% of the trials for that key, Gn was presented and after 10 s, the trial always ended without reinforcement (S-). Thus, the overall probability of reinforcement associated with the left-key, was 20% reinforcement.

In contrast, if the pairing Bl/Ye were each associated with a $P(\text{rf})$ .50 (50% reinforcement for each stimulus), it meant that each stimulus was not only presented
on the right-key with a presentation probability of .20 and .80, respectively, each stimulus was also correlated with 50% reinforcement, regardless of the stimulus displayed. For example, on 20% of the trials on the right-key, Bl was presented and on the remaining 80% of trials for that key, Ye was presented. After 10-s presentation of either stimulus, reinforcement was provided 50% of the time. Thus, the overall probability of reinforcement associated with the right-key was 50% reinforcement, irrespective of the stimulus presented.

Terminology for the two Alternative Schedules. For ease of terminology, the side key and paired stimuli associated with an overall 20% reinforcement, was called the low-probability alternative. This alternative was associated with discriminative stimuli (e.g., Rd/Gn) that reliably predicted the presence (S+) and absence (S-) of 20% reinforcement. In contrast, the side key and paired stimuli associated with the higher amount of 50% reinforcement overall, was called the non-discriminative alternative. This was because the paired stimuli (e.g., Bl/Ye) were both correlated with 50% reinforcement regardless of the stimulus presented, and therefore were unreliable predictors of the trial outcome.

Chained Procedure. Each alternative and its corresponding contingencies operated on a chained procedure on its associated side key. This procedure ensured that the effort required to obtain the discriminative stimuli that reliably predicted the presence (S+) and absence (S-) of reinforcement on the low-probability alternative, was the same as the effort required to obtain the unreliable stimuli that non-differentially signalled reinforcement on the non-discriminative alternative.

Access to each alternative and its contingencies were provided via a single response made to an illuminated white-side key (initial-link). This response
completed the initial-link requirement, and provided access to the terminal-link stimuli and its corresponding reinforcement contingencies that were associated with that key. This was signalled by an immediate change in key colour to one of two terminal-link stimuli that were associated with the alternative in effect on the respective key. The coloured stimulus was presented for a FT 10 s, after which the terminal-link ended with an outcome, either 2-s access to food or a 3-s blackout period, independent of a response.

**The Experiment**

Each session consisted of 120 trials which comprised 80 randomly alternating forced-choice trials (40 forced-choice trials to the left-key, and 40 to the right-key), with 40 choice-trials randomly presented among the forced-choice trials. Forced-choice trials ensured the hen sampled both alternatives and their corresponding contingencies on each side key, while choice-trials provided the hen with a choice between those alternatives.

**Reinforcement Ratios.** For each trial type, each stimulus within each pair was presented with a probability of .20 and .80, respectively, which resulted in eight presentations of one stimulus and 32 presentations of the other stimulus. This resulted in a reinforcement ratio of 8:0 (S+ : S-) on the low-probability alternative, and 4:16 (S+) on the non-discriminative alternative. For example, if the paired stimuli were associated with the low-probability of 20% reinforcement, the presentation probability of each stimulus resulted in a reinforcement ratio of 8:0 (S+ : S-) per trial type. This meant that of the 40 trials per trial type, reinforcement occurred eight times, and a 3-s blackout period occurred 32 times. If, however, the paired stimuli were associated with the higher non-discriminative alternative of 50%
reinforcement, the presentation of each stimulus resulted in a reinforcement ratio of 4:16 ($S^+$) per trial type. This meant that out of the 40 trials per trial type, each stimulus provided four or 16 reinforcers, and equally likely was a 3-s blackout period. Thus, each stimulus provided reinforcement or a blackout period, 50% of the time it was presented. The maximum amount of reinforcers a hen could obtain in a session (120 trials) was 48 reinforcers, and the minimum was 36.

**Forced-Choice Trials.** All trials began with an illuminated white center-key. On forced-choice trials, a single response to the center-key illuminated a white left- or right-side key (initial-link). The other side key remained dark and inoperative. The first response on the initial-link resulted in the darkening of the white light and the immediate illumination of one of two terminal-link stimuli that were associated with the alternative in effect on that key. After 10 s, the coloured stimulus was extinguished and the terminal-link ended with 2-s access to food or a 3-s blackout period. For example, if the side key was associated with the low-probability alternative, on 20% of the trials, a single response made to its corresponding initial-link key resulted in the presentation of a coloured stimulus, and after 10 s, reinforcement was always provided ($S^+$) independent of a response. On the remaining 80% of the trials, a response to the same initial-link key resulted in a second coloured stimulus and after 10 s, the trial always ended with a 3-s blackout period and no reinforcement ($S^-$). Thus, when the low-probability alternative was in effect, reliable signals predicted the presence ($S^+$) and absence ($S^-$) of 20% reinforcement.

If the side key was associated with the non-discriminative alternative, however, a response to its corresponding initial-link key resulted in a third coloured
stimulus on 20% of the trials, or a fourth coloured stimulus on the remaining 80% of the trials. After 10-s presentation of either stimulus, reinforcement or a 3-s blackout period was delivered 50% of the time, regardless of the stimulus presented. Thus, when the non-discriminative alternative was in effect, unreliable stimuli non-differentially signalled reinforcement 50% of the time.

Choice-Trials. During choice-trials, both alternatives operated simultaneously, and the hens were given a choice between the alternatives and their corresponding reinforcement contingencies. Choice-trials also began with an illuminated white center-key. A peck to the center-key simultaneously illuminated both side keys white (initial-links). A single response to either initial-link key, led to its corresponding terminal-link stimuli and reinforcement contingencies associated with the chosen side key. The other side key was rendered dark and inoperative. Choice of the initial-link was signalled by an immediate change in key colour from white to one of two coloured stimuli (for 10-s) associated with the alternative in effect on the chosen key, in the same proportion and with the same outcome as on forced-choice trials.

Terminal-Link Outcomes. During reinforcement, all key lights were extinguished and the food hopper was illuminated and raised to allow the hen 2-s access to wheat. Where trials ended without reinforcement, a brief 3-s blackout period was implemented to ensure trial lengths remained the same across trials. Following reinforcement or the blackout period, an ITI 10-s began after which the center-key was relit and the next trial began. A diagram of each series of experimental conditions used in this study, are presented in Figures 2, 3 and 4.

Experimental sessions ended after 120 trials or an hour; whichever occurred
first.

**Procedure for Conditions 1-6 (Replication Series)**

The aim of this series of conditions was to partially replicate Phases 1 and 2 of Stagner and Zentall’s (2010) procedure, and test the reliability and robustness of their findings. To discount any pre-existing preferences on the basis of side or colour biases, the paired stimuli and reinforcement contingencies associated with the side keys were repeatedly reversed across Conditions 1-4 and Condition 6.

In Condition 5, the stimuli and reinforcement contingencies were altered: The presentation probabilities associated with each stimulus and its corresponding probability of reinforcement were equated at 50%. Measures of choice performances were obtained from the proportion of times each hen chose the left-key over the right-key when given a choice (i.e., left choice / (left choice + right choice)*100). In this condition, each stimulus remained in its pair, and each pair was associated with a side key. For each pair and each trial type, one stimulus was presented for 10 s for 50% of the trials on its respective side key, and the second stimulus was presented on the remaining half of the trials on that key. After 10 s, reinforcement or a blackout period was provided 50% of the time, regardless of the stimulus presented.

A diagram of the complete series of choice procedures for experimental Conditions 1-6 is presented in Figure 3. Table 2 presents the details of this series of conditions, including the stimuli and reinforcement contingencies associated with the side keys for each condition. Each hen was exposed to each condition for a period of 12 to 40 consecutive sessions depending on the condition in effect and/or performance issues. Table 3 presents the number of sessions each hen experienced in each condition. A formal stability criterion was not employed in the present study.
Figure 3. Diagram of the complete series of choice procedures for experimental Conditions 1-6. Refer to the replication series section for further details.
Table 2. Order of experimental Conditions 1-6, the side key each alternative was presented on, its associated paired stimuli and their probability of presentation and corresponding probability of reinforcement. Note that in Condition 5 (L-50/50 10:10), there was no low-probability alternative, as the presentation probability of each stimulus and its corresponding probability of reinforcement, was equated at 50%.

<table>
<thead>
<tr>
<th>Condition</th>
<th>Low-Probability Alternative of 20% Reinforcement</th>
<th>Non-Discriminative Alternative of 50% Reinforcement</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Side Key</td>
<td>Side Key</td>
</tr>
<tr>
<td></td>
<td>100% S+ / 0% S-</td>
<td>S+ / S-</td>
</tr>
<tr>
<td>1. L-Rd/Gn 8:0</td>
<td>Left</td>
<td>Red/Green</td>
</tr>
<tr>
<td>2. R-Rd/Gn 8:0</td>
<td>Right</td>
<td>Red/Green</td>
</tr>
<tr>
<td>3. L-Bl/Ye 8:0</td>
<td>Left</td>
<td>Blue/Yellow</td>
</tr>
<tr>
<td>4. R-Bl/Ye 8:0</td>
<td>Right</td>
<td>Blue/Yellow</td>
</tr>
<tr>
<td>5. L-50/50 10:10</td>
<td></td>
<td></td>
</tr>
<tr>
<td>6. R-Bl/Ye 8:0</td>
<td>Right</td>
<td>Blue/Yellow</td>
</tr>
</tbody>
</table>

Note. Condition labels (e.g., L-Rd/Gn 8:0) show the side (L = Left, R = Right) and paired stimuli associated with the low-probability alternative (e.g., Rd/Gn = Red/Green, Bl/Ye = Blue/Yellow). The ratios (e.g., 8:0), indicate the ratio of reinforcement (S+) to no reinforcement (S-) for each low-probability stimulus (e.g., S+ : S- = Rd/Gn 8:0) for each condition except Condition 5, where stimuli and reinforcement probabilities were equated at 50% resulting in a reinforcement ratio of 10:10 (S+) for each stimulus; 100% S+ / 0% S- = stimulus that reliably signalled reinforcement (S+) and no reinforcement (S-); P S+ / S- = presentation probability of S+ and S- stimuli; P(rf) S+ / S- = probability of reinforcement associated with S+ and S- stimuli; 50% S1 / S2 = stimuli 1 and stimuli 2 which non-differentially signalled 50% reinforcement; P S1 / S2 = presentation probability of stimuli 1 and stimuli 2; P(rf) S1 / S2 = probability of reinforcement associated with stimuli 1 and stimuli 2.
Table 3. *Number of sessions each subject experienced in Conditions 1-6.*

<table>
<thead>
<tr>
<th></th>
<th>Hen</th>
<th>Actual Days</th>
<th>Consecutive Sessions</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Condition</strong></td>
<td><strong>Hen</strong></td>
<td><strong>Actual Days</strong></td>
<td><strong>Consecutive Sessions</strong></td>
</tr>
<tr>
<td>1. L-Rd/Gn 8:0</td>
<td>12.1</td>
<td>84</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>12.2</td>
<td>21</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>12.3</td>
<td>21</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>12.4</td>
<td>21</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td>12.5</td>
<td>18</td>
<td>19</td>
</tr>
<tr>
<td></td>
<td>12.6</td>
<td>21</td>
<td>19</td>
</tr>
<tr>
<td>2. R-Rd/Gn 8:0</td>
<td>12.1</td>
<td>22</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>12.2</td>
<td>26</td>
<td>19</td>
</tr>
<tr>
<td></td>
<td>12.3</td>
<td>22</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>12.4</td>
<td>24</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>12.5</td>
<td>20</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>12.6</td>
<td>18</td>
<td>15</td>
</tr>
<tr>
<td>3. L-Bl/Ye 8:0</td>
<td>12.1</td>
<td>17</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>12.2</td>
<td>15</td>
<td>13</td>
</tr>
<tr>
<td></td>
<td>12.3</td>
<td>15</td>
<td>12</td>
</tr>
<tr>
<td></td>
<td>12.4</td>
<td>15</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>12.5</td>
<td>15</td>
<td>13</td>
</tr>
<tr>
<td></td>
<td>12.6</td>
<td>23</td>
<td>14</td>
</tr>
<tr>
<td>4. R-Bl/Ye 8:0</td>
<td>12.1</td>
<td>18</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>12.2</td>
<td>19</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>12.3</td>
<td>14</td>
<td>12</td>
</tr>
<tr>
<td></td>
<td>12.4</td>
<td>17</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>12.5</td>
<td>31</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>12.6</td>
<td>17</td>
<td>15</td>
</tr>
<tr>
<td>5. L-50/50 10:10</td>
<td>12.1</td>
<td>36</td>
<td>30</td>
</tr>
<tr>
<td></td>
<td>12.2</td>
<td>36</td>
<td>29</td>
</tr>
<tr>
<td></td>
<td>12.3</td>
<td>48</td>
<td>30</td>
</tr>
<tr>
<td></td>
<td>12.4</td>
<td>73</td>
<td>30</td>
</tr>
<tr>
<td></td>
<td>12.5</td>
<td>36</td>
<td>28</td>
</tr>
<tr>
<td></td>
<td>12.6</td>
<td>35</td>
<td>29</td>
</tr>
<tr>
<td>6. R-Bl/Ye 8:0</td>
<td>12.1</td>
<td>19</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>12.2</td>
<td>18</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>12.3</td>
<td>24</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>12.4</td>
<td>15</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>12.5</td>
<td>24</td>
<td>19</td>
</tr>
<tr>
<td></td>
<td>12.6</td>
<td>20</td>
<td>16</td>
</tr>
</tbody>
</table>

*Note.* Condition labels (e.g., L-Rd/Gn 8:0) shows the side (L = Left, R = Right) and paired stimuli associated with the low-probability alternative (e.g., Rd/Gn = Red/Green, Bl/Ye = Blue/Yellow). The ratios (e.g., 8:0), indicate the ratio of reinforcement (S+) to no reinforcement (S-) for each low-probability stimulus (e.g., Rd, 8 : Gn, 0) for each condition except for Condition 5, where stimuli and reinforcement probabilities were equated at 50% resulting in a reinforcement ratio of 10:10 (S+) for each stimulus.
In prior experiments of similar types, pigeons were usually exposed to each condition for a period of 12, 25 or 40 sessions which appeared to be sufficient for response allocation to stabilise (e.g., Stagner & Zentall, 2010; Stagner et al., 2012; Zentall & Stagner, 2011a; Zentall & Stagner 2011b).

**Condition 1: L-Rd/Gn 8:0 Procedure.** The choice procedure for Condition 1 is illustrated in the top panel of Figure 3. In Condition 1, the low-probability alternative was presented on the left-key using Rd and Gn stimuli which reliably predicted the presence (S+, Rd) and absence (S-, Gn) of 20% reinforcement. The non-discriminative alternative was presented on the right-key using Bl and Ye stimuli which non-differentially signalled 50% reinforcement regardless of the stimulus presented.

**Condition 2: R-Rd/Gn 8:0 Procedure.** The choice procedure for Condition 2 is illustrated in second panel from the top, of Figure 3. The procedure for Condition 2 was the same as Condition 1, except that the side keys that were previously associated with each alternative were reversed. In this condition, the reliable stimuli (Rd/Gn) associated with the low-probability alternative was presented on the right-key. The unreliable stimuli (Bl/Ye) associated with the non-discriminative alternative was presented on the left-key. This condition was implemented to ensure any pre-existing side preferences were ruled out rather than the reinforcement contingencies associated with each side key.

**Condition 3: L-Bl/Ye 8:0 Procedure.** The choice procedure for Condition 3 is illustrated in third panel from the top, of Figure 3. The procedure for Condition 3 was the same as that for Condition 1, except that the paired stimuli and reinforcement contingencies associated with each alternative were reversed. In Condition 3, the
low-probability alternative was presented on the left-key using Bl and Ye stimuli which reliably signalled the presence (S+, Bl) and absence (S-, Ye) of 20% reinforcement. The paired stimuli, Rd and Gn, was associated with the non-discriminative alternative of 50% reinforcement and were presented on the right-key. The aim of this condition was to rule out any pre-existing colour preferences that may have developed.

*Conditions 4 and 6: R-Bl/Ye 8:0 Procedures.* The choice procedure for Conditions 4 and 6 is illustrated in the fourth, and bottom panels of Figure 3. The procedure for both conditions was the same as Condition 3, except that the side keys that were previously associated with each alternative were reversed. In Conditions 4 and 6, the reliable stimuli (Bl/Ye) associated with the low-probability alternative of 20% reinforcement was presented on the right-key. The unreliable stimuli (Rd/Gn) associated with the non-discriminative alternative of 50% reinforcement, was presented on the left-key. Conditions 4 and 6 acted as an ABA design.

*Condition 5: L-50/50 10:10 Procedure.* The choice procedure for Condition 5 is presented in the second panel from the bottom of Figure 3. The procedure used in Condition 5 differed from previous conditions in the following ways. In this condition, the paired stimuli were associated with a side key; Bl and Ye stimuli were presented on the left-key, while Rd and Gn were presented on the right-key. For each pair, however, the presentation probabilities associated with each stimulus and its corresponding probability of reinforcement were equated at 50%. This meant that for each pair, one stimulus was presented for 50% of the trials on its respective side key, and the second stimulus was presented for the remaining half of the trials for that key. After 10 s, reinforcement or a blackout period was provided 50% of the time the
stimulus was presented.

This configuration resulted in a reinforcement ratio of 10:10 (S+) for each stimulus and trial type. In Condition 5, the maximum amount of reinforcers a hen could obtain in a session (120 trials) was 60 reinforcers; 20 reinforcers from each pair of stimuli per trial type. Thus, the presentation probability of each stimulus and its corresponding probability of reinforcement were held constant at 50% for this condition. The aim of Condition 5 was to assess choice performances across the side keys when reliable signals for reinforcement were withheld.

**Procedure for Conditions 7-11 (Reliability of Stimuli Series)**

The aim of this series of conditions was to partially replicate Phase 4 of Stagner and Zentall’s (2010) procedure, and assess the point at which the subjects would choose the non-discriminative alternative over the low-probability alternative when the reliability of the stimuli that differentially predicted 20% reinforcement, was gradually made less reliable over a series of conditions.

Conditions 7-11 were conducted in the same way as the previous series of conditions, using the same technical procedures as those shown in Figure 1. Each stimulus remained in its pair (Rd/Gn and Bl/Ye), and the overall probability of reinforcement associated with the alternatives was not altered across Conditions 7-11 (i.e., 20% and 50% reinforcement). The only procedural difference from the previous series of conditions was that in Conditions 7-11, the side keys on which the alternatives appeared, including the paired stimuli associated with each alternative, remained the same across conditions. Another difference was that the stimuli that reliably predicted the presence (S+) and absence (S-) of reinforcement on the low-probability alternative, was progressively made less reliable across conditions. The
non-discriminative alternative which used unreliable signals for reinforcement was left unchanged.

For this series of conditions, the non-discriminative alternative was presented on the right-key using Bl and Ye stimuli which non-differentially signalled 50% reinforcement regardless of the stimulus presented. The low-probability alternative of 20% reinforcement was presented on the left-key using Rd and Gn stimuli. The presentation probability of each low-probability stimulus (Rd/Gn) remained at .20 and .80, respectively. The probability of reinforcement associated with each stimulus, however, was altered: With each condition, the reliability of Rd which previously signalled reinforcement (S+, Rd) on the low-probability alternative every time it was presented, was progressively reduced from a $P_{rf}$ 1.0 to .50, across conditions, while Gn, which previously signalled no reinforcement (S-, Gn), was progressively raised from a $P_{rf}$ 0.0 to .50 with each condition. This configuration resulted in a corresponding change to the reinforcement ratio for each low-probability stimulus which ranged from 8:0 to 4:4 (e.g., S+ : S-/+, respectively).

This meant, for example, that each low-probability stimulus was presented with a probability of .20 and .80, respectively. In addition, each stimulus had a corresponding probability of reinforcement of $P_{rf}$ 1.0 and 0.0, respectively. Under this arrangement, eight presentations of Rd occurred per trial type, with 32 presentations of Gn. This resulted in a ratio of reinforcement to no reinforcement of 8:0 (S+ : S-), respectively. Thus, every presentation of Rd provided reinforcement (S+), while Gn did not (S-). If the low-probability stimuli, however, had a corresponding probability of reinforcement of $P_{rf}$ .50 each, the resulting reinforcement ratio for each stimulus was 4:4 (S+ : S+), respectively. This meant that
of the eight presentations of Rd for each trial type, only four provided reinforcement whereas four of the 32 presentations of Gn now provided reinforcement as well. Thus, the low-probability alternative retained its overall 20% reinforcement, despite the reliability of its corresponding stimuli becoming less reliable signals for 20% reinforcement across conditions.

A diagram of the complete series of choice procedures for experimental Conditions 7-11, is presented in Figure 4. Table 4 presents the details of this series of conditions, including the probability of reinforcement and corresponding reinforcement ratio for each stimulus in each alternative, for Conditions 7-11. Table 5 presents the number of sessions each hen experienced in each condition.

**Condition 7: L-Rd/Gn 7:1 Procedure.** The choice procedure for Condition 7 is illustrated in the top panel of Figure 4. In Condition 7, the probability of reinforcement associated with Rd and Gn was $P(\text{rf}) .90$ and .10, respectively. This resulted in a reinforcement ratio of 7:1 for each stimulus.

**Condition 8: L-Rd/Gn 8:0 Procedure.** The choice procedure for Condition 8 is illustrated in the second panel from the top, of Figure 4. The procedure for Condition 8 was identical to Condition 1. In Condition 8, Rd and Gn were associated with a reinforcement probability of $P(\text{rf}) 1.0$ and 0.0, respectively. This corresponded to a reinforcement ratio of 8:0 (S+ : S-) for each stimulus. Thus, the reliability of Rd and Gn, reliably predicting the presence (S+, Rd) and absence (S-, Gn) of 20% reinforcement on the low-probability alternative, was reinstated.

**Condition 9: L-Rd/Gn 6:2 Procedure.** The choice procedure for Condition 9 is illustrated in the third panel of Figure 4. In this condition, the reinforcement contingencies associated with Rd and Gn was altered to $P(\text{rf}) .80$ and .20,
Figure 4. Diagram of the complete series of choice procedures for experimental Conditions 7-11. The low-probability alternative of 20% reinforcement was presented on the left-key using red and green stimuli, and the non-discriminative alternative of 50% reinforcement was presented on the right-key using blue and yellow stimuli. The number of coloured circles in each condition represents the reinforcement ratio for each stimulus in each alternative.
Table 4. Order of experimental Conditions 7-11, and the presentation probability of each stimulus in each alternative, including its corresponding probability of reinforcement and reinforcement ratio. The low-probability alternative of 20% reinforcement was presented on the left-key using red (Rd) and green (Gn) stimuli. The higher non-discriminative alternative of 50% reinforcement was presented on the right-key and was signalled by blue (Bl) and yellow (Ye) stimuli.

<table>
<thead>
<tr>
<th>Condition</th>
<th>LEFT KEY (Low-Probability Alternative of 20% Reinforcement)</th>
<th>RIGHT KEY (Non-Discriminative Alternative of 50% Reinforcement)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( P_{\text{Rd/Gn}} )</td>
<td>( P(\text{rf})_{\text{Rd/Gn}} )</td>
</tr>
<tr>
<td>7. L-Rd/Gn 7:1</td>
<td>.20 / .80</td>
<td>.90 / .10</td>
</tr>
<tr>
<td>8. L-Rd/Gn 8:0</td>
<td>.20 / .80</td>
<td>1.0 / 0.0</td>
</tr>
<tr>
<td>9. L-Rd/Gn 6:2</td>
<td>.20 / .80</td>
<td>.80 / .20</td>
</tr>
<tr>
<td>10. L-Rd/Gn 5:3</td>
<td>.20 / .80</td>
<td>.60 / .40</td>
</tr>
<tr>
<td>11. L-Rd/Gn 4:4</td>
<td>.20 / .80</td>
<td>.50 / .50</td>
</tr>
</tbody>
</table>

Note. Condition labels (e.g., L-Rd/Gn 7:1) shows the side (L = Left) and paired stimuli associated with the low-probability alternative (e.g., Rd/Gn = Red/Green). The non-discriminative alternative was presented on the right-key using blue (Bl) and yellow (Ye) stimuli that non-differentially signalled 50% reinforcement. The ratios (e.g., 7:1) indicate the reinforcement ratio for each low-probability stimulus (e.g., Rd, 7 : Gn, 1) for each condition; \( P_{\text{Rd/Gn}} \) = presentation probability of red (Rd) and green (Gn) stimuli; \( P(\text{rf})_{\text{Rd/Gn}} \) = probability of reinforcement associated with red and green stimuli; \( \text{Ratio(\text{rf})}_{\text{Rd : Gn}} \) = reinforcement ratio of red to green; \( P_{\text{Bl/Ye}} \) = presentation probability of blue (Bl) and yellow (Ye) stimuli, \( P(\text{rf})_{\text{Bl/Ye}} \) = probability of reinforcement associated with blue and yellow; \( \text{Ratio(\text{rf})}_{\text{Bl : Ye}} \) = reinforcement ratio of blue to yellow. Note that the \( \text{Ratio(\text{rf})} \) of each stimulus was rounded to the nearest whole number for reinforcer delivery.
Table 5. *Number of sessions each subject experienced in Conditions 7-11.*

<table>
<thead>
<tr>
<th>Experimental Conditions 7-11</th>
<th>Condition</th>
<th>Hen</th>
<th>Actual Days</th>
<th>Consecutive Sessions</th>
<th>Condition</th>
<th>Hen</th>
<th>Actual Days</th>
<th>Consecutive Sessions</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>7. L-Rd/Gn 7:1</td>
<td>12.1</td>
<td>37</td>
<td>30</td>
<td>7. L-Rd/Gn 7:1</td>
<td>12.1</td>
<td>15</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td></td>
<td>12.2</td>
<td>48</td>
<td>40</td>
<td>10. L-Rd/Gn 5:3</td>
<td>12.2</td>
<td>17</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td></td>
<td>12.3</td>
<td>34</td>
<td>30</td>
<td></td>
<td>12.3</td>
<td>15</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td></td>
<td>12.4</td>
<td>35</td>
<td>30</td>
<td></td>
<td>12.4</td>
<td>17</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td></td>
<td>12.5</td>
<td>49</td>
<td>33</td>
<td></td>
<td>12.5</td>
<td>39</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td></td>
<td>12.6</td>
<td>49</td>
<td>32</td>
<td></td>
<td>12.6</td>
<td>20</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>8. L-Rd/Gn 8:0</td>
<td>12.1</td>
<td>19</td>
<td>15</td>
<td>10. L-Rd/Gn 5:3</td>
<td>12.1</td>
<td>17</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td></td>
<td>12.2</td>
<td>20</td>
<td>14</td>
<td></td>
<td>12.2</td>
<td>21</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td></td>
<td>12.3</td>
<td>17</td>
<td>15</td>
<td></td>
<td>12.3</td>
<td>22</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td></td>
<td>12.4</td>
<td>16</td>
<td>15</td>
<td></td>
<td>12.4</td>
<td>23</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td></td>
<td>12.5</td>
<td>17</td>
<td>15</td>
<td></td>
<td>12.5</td>
<td>18</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td></td>
<td>12.6</td>
<td>16</td>
<td>15</td>
<td></td>
<td>12.6</td>
<td>25</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td></td>
<td>12.2</td>
<td>17</td>
<td>15</td>
<td></td>
<td>12.2</td>
<td>21</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td></td>
<td>12.3</td>
<td>19</td>
<td>15</td>
<td></td>
<td>12.3</td>
<td>22</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td></td>
<td>12.4</td>
<td>16</td>
<td>15</td>
<td></td>
<td>12.4</td>
<td>23</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td></td>
<td>12.5</td>
<td>39</td>
<td>15</td>
<td></td>
<td>12.5</td>
<td>18</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td></td>
<td>12.6</td>
<td>29</td>
<td>15</td>
<td></td>
<td>12.6</td>
<td>25</td>
<td>15</td>
</tr>
</tbody>
</table>

*Note.* Condition labels (e.g., L-Rd/Gn 7:1) shows the side (L = Left) and paired stimuli associated with the low-probability alternative (Rd/Gn = Red/Green). The ratios (e.g., 7:1) indicate the reinforcement ratio for each low-probability stimulus (e.g., Rd, 7 : Gn, 1) for each condition.
respectively, which resulted in a reinforcement ratio of 6:2 for each stimulus.

**Condition 10: L-Rd/Gn 5:3 Procedure.** The choice procedure for Condition 10 is presented in the second panel from the bottom, of Figure 4. In this condition, the reinforcement contingencies associated with Rd and Gn were altered to \( P(\text{rf}) .60 \) and .40, respectively, which resulted in a reinforcement ratio of 5:3 for each stimulus.

**Condition 11: L-Rd/Gn 4:4 Procedure.** The choice procedure for Condition 11 is illustrated in the bottom panel of Figure 4. The procedure for Condition 11 was almost identical to that of the non-discriminative alternative, except that the overall reinforcement of 20% was retained on the low-probability alternative. In this condition, the probability of reinforcement associated with Rd and Gn was \( P(\text{rf}) .50 \) (or 50% reinforcement for each stimulus). This resulted in a reinforcement ratio of 4:4, respectively.

**Procedure for Conditions 12 and 13 (Controls for Bias Series)**

The aim of this series of conditions was to rule out side and colour biases, and assess the point at which the subjects would choose the non-discriminative alternative over the low-probability alternative when the reliability of the low-probability stimuli, was made unreliable within two conditions. In this series of conditions, the procedures of Conditions 8 and 11 from the previous series of conditions were reversed (Conditions 12 and 13, respectively). Thus, this series of conditions was a partial combination of Phases 2 and 4 of Stagner and Zentall’s (2010) procedure.

Conditions 12 and 13 were conducted in the same way as the previous series of conditions, using the same technical procedures as those shown in Figure 1. Each stimulus remained in its pair (Rd/Gn and Bl/Ye), and the overall rate of reinforcement associated with each alternative was not altered for Conditions 12 and 13. The only
procedural differences to Conditions 7-11 was that the paired stimuli and reinforcement contingencies associated with the side keys were reversed in Conditions 12 and 13 (see Table 6, cf., Table 4), and the stimuli that reliably predicted the presence (S+) and absence (S-) of reinforcement on the low-probability alternative, was made unreliable from Conditions 12 to 13. The non-discriminative alternative which used unreliable signals for reinforcement was left unchanged.

For both conditions, the non-discriminative alternative of 50% reinforcement was presented on the left-key using Rd and Gn stimuli, and the low-probability alternative of 20% reinforcement was presented on the right-key using Bl and Ye stimuli. While the presentation probability for each low-probability stimulus (Bl/Ye) remained the same, either .20 and .80, respectively, the corresponding probability of reinforcement associated with each stimulus was altered from P(rf) 1.0 and 0.0 in Condition 12, to P(rf) .50 each, in Condition 13. This configuration resulted in a corresponding change to the reinforcement ratio for each low-probability stimulus which was 8:0 (S+ : S-), respectively, in Condition 12, and 4:4 (S+ : S+), respectively, in Condition 13.

Under this arrangement, this meant that of the eight presentations of Bl, and 32 presentations of Ye per trial type, Bl always provided reinforcement (S+) in Condition 12, while Ye did not (S-). In Condition 13, however, it meant that of the eight presentations of Bl for every trial type, only four provided reinforcement whereas four of the 32 presentations of Ye now provided reinforcement as well. Thus, the low-probability alternative retained its overall 20% reinforcement despite the reliability of its corresponding stimuli becoming unreliable signals for reinforcement across conditions.
Another aim of this series of experiments was to investigate the presence of hysteresis in the data. Because performance in subsequent conditions can be influenced by the contingencies experienced in previous conditions, it was thought that the presence of hysteresis would provide an alternative measure of each subject’s preference for reliable signals for reinforcement, rather than the reinforcement contingencies associated with each alternative (Davidson & Baum, 2000). For example, a short transitional period from an old, to a new stable state of responding on the low-probability alternative would suggest a strong preference for reliable signals that differentially predict 20% reinforcement, while longer transitions would suggest a weaker preference for those signals.

A diagram of the complete series of choice procedures for experimental Conditions 12 and 13 are presented in Figure 5. Table 6 presents the details of this series of conditions, including the probability of reinforcement and corresponding reinforcement ratio for each stimulus in each alternative, for each condition. Table 7 presents the number of sessions each hen experienced in each condition.

**Condition 12: R-Bl/Ye 8:0 Procedure.** The choice procedure for Condition 12 is illustrated in the top panel of Figure 5. In this condition, the probability of reinforcement associated with Bl and Ye was $P_{rf} = 1.0$ and 0.0, respectively, which resulted in a reinforcement ratio of 8:0 ($S_+ : S_-$), for each stimulus. Thus, the reliability of Bl and Ye reliably predicting the presence ($S_+$, Bl) and absence ($S_-$, Ye) of 20% reinforcement on the low-probability alternative was reinstated.

**Condition 13: R-Bl/Ye 4:4 Procedure.** The choice procedure for Condition 13 is illustrated in the bottom panel of Figure 5. The procedure for Condition 13 was almost identical to that of the non-discriminative alternative, except that the overall
reinforcement of 20% was retained on the low-probability alternative. In this condition, the probability of reinforcement associated with Bl and Ye was $P(rf) .50$ (or 50% reinforcement for each stimulus). This resulted in a reinforcement ratio of 4:4, respectively.
Figure 5. Diagram of the choice procedures for experimental Conditions 12 and 13. The low-probability alternative of 20% reinforcement was presented on the right-key using blue and yellow stimuli and the non-discriminative alternative of 50% reinforcement was presented on the left-key using red and green stimuli. The number of coloured circles in each condition represents the reinforcement ratio of each stimulus in each alternative.
Table 6. Order of experimental Conditions 12 and 13, and the presentation probability of each stimulus in each alternative, including its corresponding probability of reinforcement and reinforcement ratio. The low-probability alternative of 20% reinforcement was presented on the right-key using blue (Bl) and yellow (Ye) stimuli. The higher non-discriminative alternative of 50% reinforcement was presented on the left-key and was signalled by red (Rd) and green (Gn) stimuli.

<table>
<thead>
<tr>
<th>Condition</th>
<th>LEFT KEY</th>
<th></th>
<th>RIGHT KEY</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Non-Discriminative Alternative of 50% Reinforcement</td>
<td>Low-Probability Alternative of 20% Reinforcement</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$P_{Rd / Gn}$</td>
<td>$P_{rf, Rd / Gn}$</td>
<td>$Ratio_{rf, Rd : Gn}$</td>
</tr>
<tr>
<td>12. R-Bi/Ye 8:0</td>
<td>.20 / .80</td>
<td>.50 / .50</td>
<td>4 : 16</td>
<td>.20 / .80</td>
</tr>
<tr>
<td>13. R-Bi/Ye 4:4</td>
<td>.20 / .80</td>
<td>.50 / .50</td>
<td>4 : 16</td>
<td>.20 / .80</td>
</tr>
</tbody>
</table>

*Note.* Condition labels (e.g., R-Bi/Ye 8:0) shows the side (R = Right) and paired stimuli associated with the low-probability alternative (e.g., Bl/Ye = Blue/Yellow). The non-discriminative alternative was presented on the left-key using red (Rd) and green (Gn) stimuli. The ratios (e.g., 8:0), indicate the reinforcement ratio for each low-probability stimulus (e.g., Bl, 8 : Ye, 0) for each condition; $P_{Rd / Gn}$ = presentation probability of red (Rd) and green (Gn) stimuli; $P_{rf, Rd / Gn}$ = probability of reinforcement associated with red and green; $Ratio_{rf, Rd : Gn}$ = reinforcement ratio of red to green; $P_{Bl / Ye}$ = presentation probability of blue (Bl) and yellow (Ye) stimuli; $P_{rf, Bl / Ye}$ = probability of reinforcement associated with blue and yellow stimuli; $Ratio_{rf, Bl : Ye}$ = reinforcement ratio of blue to yellow. Note that the $Ratio_{rf}$ of each stimulus was rounded to the nearest whole number for reinforcer delivery.
Table 7. *Number of sessions each subject experienced in Conditions 12 and 13.*

<table>
<thead>
<tr>
<th>Condition</th>
<th>Hen</th>
<th>Actual Days</th>
<th>Consecutive Sessions</th>
<th>Condition</th>
<th>Hen</th>
<th>Actual Days</th>
<th>Consecutive Sessions</th>
</tr>
</thead>
<tbody>
<tr>
<td>12.2</td>
<td>17</td>
<td>15</td>
<td>12.2</td>
<td>28</td>
<td>25</td>
<td></td>
<td></td>
</tr>
<tr>
<td>12.3</td>
<td>15</td>
<td>15</td>
<td>12.3</td>
<td>32</td>
<td>25</td>
<td></td>
<td></td>
</tr>
<tr>
<td>12.4</td>
<td>15</td>
<td>15</td>
<td>12.4</td>
<td>34</td>
<td>25</td>
<td></td>
<td></td>
</tr>
<tr>
<td>12.5</td>
<td>16</td>
<td>15</td>
<td>12.5</td>
<td>38</td>
<td>25</td>
<td></td>
<td></td>
</tr>
<tr>
<td>12.6</td>
<td>15</td>
<td>15</td>
<td>12.6</td>
<td>26</td>
<td>25</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Note.* Condition labels (e.g., R-Bl/Ye 8:0) shows the side (R = Right) and paired stimuli associated with the low-probability alternative (Bl/Ye = Blue/Yellow). The ratios (e.g., 8:0), indicate the reinforcement ratio for each low-probability stimulus (e.g., Bl, 8 : Ye, 0) for each condition.
Results

Only data from the choice-trials of each session and each condition have been analysed and presented here. The complete data set for all trials and all conditions are presented in Appendix A. Choice trial data were the number of times the low-probability or left-key alternative (depending on the condition) was chosen when a hen was given a choice between two concurrently available schedules. The low-probability alternative was generally associated with stimuli which reliably predicted the presence (S+) and absence (S-) of 20% reinforcement (see Table 2, cf., Tables 4 and 6). The non-discriminative alternative was associated with unreliable stimuli which non-differentially signalled a higher probability of 50% reinforcement.

Choice-trial data for each subject from each session, in each series of conditions, are presented in Figures 6, 7 and 8. Choice performances were analysed by calculating the percentage of responses made to the side key that was associated with the low-probability (or left-key) alternative. Choice percentages were calculated by dividing the number of responses made on the low-probability (or left-key) alternative per session, by the sum of responses made to both alternatives (e.g., left choice / (left choice + right choice), multiplied by 100. Choice performances in Condition 5 were the number of times the subject chose the left-key over the right-key when the presentation probability of each stimulus and its corresponding probability of reinforcement, was equated at 50%. For all graphs, percentage choice for the low-probability (and left-key) alternative is shown on the Y-axes and consecutive sessions are displayed on the X-axes. The dotted horizontal line indicates 50% choice (or point of indifference) between the alternatives, and the
dotted vertical lines indicate condition changes. Each data point represents each subject’s percentage of choice for the low-probability (or left-key) alternative for each session.

When choice percentages for the low-probability alternative was at 100%, the subject exclusively chose the option associated with reliable stimuli that differentially predicted 20% reinforcement, over an alternative associated with unreliable stimuli that non-differentially signalled 50% reinforcement. When choice percentages for the low-probability alternative fell below 50%, the subject increasingly chose the non-discriminative alternative associated with unreliable stimuli and a higher probability of 50% reinforcement. When choice percentages fell on or near 50% choice for the low-probability alternative, the subject was indifferent between the alternatives.

Results for Conditions 1-6 (Replication Series)

Figure 6 presents the percentage of choice for the low-probability (and left-key) alternative for all subjects across Conditions 1-6. Overall, results for this series of conditions show that most hens consistently chose the alternative associated with reliable stimuli that differentially predicted 20% reinforcement, over an alternative associated with unreliable stimuli that non-differentially signalled 50% reinforcement. In addition, choice for this option was almost exclusive for most subjects in most conditions. In contrast, when the presentation probability of each stimulus and its corresponding probability of reinforcement, was equated at 50% (in Condition 5), previous choice performances for all subjects, was disrupted.

Condition 1: L-Rd/Gn 8:0 Results. In Condition 1, the low-probability alternative was presented on the left-key using Rd and Gn stimuli which differentially predicted 20% reinforcement. The non-discriminative was presented on the right-key
Figure 6. Percentage of choice responses for the low-probability (20%) or left-key alternative of reinforcement, over a non-discriminative alternative of 50% reinforcement, plotted across consecutive sessions for each hen, across Conditions 1-6. The condition labels (e.g., L-Rd/Gn 8:0) along the top of the figure show the side (L = Left, R = Right) and the paired stimuli associated with the low-probability alternative (Rd/Gn = Red/Green, Bl/Ye = Blue/Yellow). The ratios (e.g., 8:0), indicate the reinforcement ratio for each low-probability stimulus (e.g., S+ : S- = Rd/Gn 8:0) for each condition. In Condition 5, the label L-50 / 50 indicate that the presentation probability of each stimulus and its corresponding probability of reinforcement, was equated at 50%. The results for Condition 5 were obtained from the percentage of choice for the left-key over the right-key.
using Bl and Ye stimuli which non-differentially signalled 50% reinforcement. The results for Condition 1 are presented in the first panel of Figure 6.

Results show that choice for the low-probability alternative was initially variable for all subjects. With the exception of Hen 12.1, results generally show that choice for this option for all hens, became consistent from Session 5 onwards; by Session 10, the hens were exclusively choosing the low-probability alternative associated with reliable stimuli. Hen 12.1, however, required 12 sessions before choice for the low-probability alternative began to increase, reaching 100% performance on this option with higher sessions.

**Condition 2: R-Rd/Gn 8:0 Results.** The procedure for Condition 2 was similar to Condition 1; except that the stimuli and reinforcement contingencies associated the side keys were reversed. In Condition 2, the reliable stimuli (Rd/Gn) associated with the low-probability alternative was presented on the right-key. The unreliable stimuli (Bl/Ye) associated with the non-discriminative alternative was presented on the left-key. The second panel of Figure 6 presents the data obtained for Condition 2.

When the stimuli and reinforcement contingencies associated with the side keys were reversed, choice for the low-probability alternative became exclusive and stable for all subjects by the third session, except Hen 12.1. Data obtained for Hen 12.1 shows that choice for this option increased and became steady and relatively stable across fewer sessions than the previous condition (e.g., 6 sessions in Condition 2 vs., 12 sessions in Condition 1).

**Condition 3: L-Bl/Ye Results.** The procedure for Condition 3 was similar to the previous condition except that the paired stimuli associated with the reinforcement contingencies were reversed. In this condition, the low-probability
alternative was presented on the left-key using Bl and Ye stimuli which reliably predicted the presence (S+, Bl) and absence (S-, Ye) of 20% reinforcement. The non-discriminative alternative was presented on the right-key using Rd and Gn stimuli which non-differentially signalled 50% reinforcement. The results for Condition 3 are presented in the third panel of Figure 6.

In Condition 3, greater variability in each subject’s choice for the low-probability alternative was observed; however, choice for the low-probability alternative generally increased across sessions and remained high and relatively stable. In contrast, choice for the low-probability alternative for Hens 12.1 and 12.5 remained at or near zero for this condition. Results for these hens in this condition indicate that they almost exclusively chose the non-discriminative alternative associated with 50% reinforcement and unreliable stimuli.

**Condition 4: R-Bl/Ye Results.** The procedure for Condition 4 was similar to Condition 3; except that the stimuli and reinforcement contingencies associated the side keys were reversed. In Condition 4, the reliable stimuli (Bl/Ye) associated with the low-probability alternative was presented on the right-key. The unreliable stimuli (Rd/Gn) associated with the non-discriminative alternative was presented on the left-key. The fourth panel of Figure 6 presents the data obtained for Condition 4.

The results varied across subjects in Condition 4. Data for Hens 12.2, 12.3, and 12.5 show a sharp increase in choice for the low-probability alternative in relatively fewer sessions than previous conditions which remained exclusive and stable. Although Hens 12.4 and 12.6 show an increasing trend for this option, with increasing sessions, Hen 12.4 displays fluctuations in choice between the alternatives towards the end of this condition. Hen 12.1 shows an initial decrease in choice for
the low-probability alternative which remained at or below 50% choice for this option for this condition, with some fluctuations and variability in the middle and final few sessions.

**Condition 5: L-50/50 Results.** The procedure for Condition 5 was unlike previous conditions; the presentation probability of each stimulus and its corresponding probability of reinforcement, was equated at 50%. In this condition, Bl and Ye stimuli were presented on the left-key and Rd and Gn stimuli were presented on the right-key. Data for Condition 5 were derived from the proportion of times each subject chose the left-key over the right-key when given a choice (left choice / (left choice + right choice)*100). The results for Condition 5 are presented in the fifth panel of Figure 6. When choice for the left-key was at 100%, the subject exclusively chose the left-key over the right-key; when choice percentages for the left-key fell below 50%, the subject increasingly chose the right-key; and when choice for the left-key fell at or near 50%, the subject was indifferent between the side keys.

The results obtained for Condition 5 varied across sessions and subjects. Choice for the left-key for each subject generally remained low, at or near zero (Hen 12.1); decreased across sessions, oscillating around 50% choice (Hen 12.2); dramatically fluctuated between alternatives (Hen 12.3); increased across sessions (Hen 12.5); or remained relatively high (Hens 12.4 and 12.6) before decreasing across remaining sessions (Hen 12.6).

**Condition 6: R-Bl/Ye Results.** The procedure for Condition 6 was identical to Condition 4. In Condition 6, the low-probability alternative was reinstated and presented on the right-key using Bl and Ye stimuli which reliably predicted the
presence (S+, Bl) and absence (S-, Ye) of 20% reinforcement. The non-discriminative alternative associated with 50% reinforcement and unreliable stimuli (Rd/Gn), was presented on the left-key. The results for Condition 6 are presented in the last panel of Figure 6. Overall, results show that when reliable signals for 20% reinforcement were reinstated, choice for the low-probability alternative became relatively exclusive and stable for all subjects by Session 2.

To summaries, Figure 6 shows that choice for the low-probability alternative was exclusive for most hens in most conditions. In particular, choice for this option for most hens held when the stimuli associated with the side keys was reversed (as in Conditions 2 and 4), and when the paired stimuli associated with the reinforcement contingencies were reversed (as in Conditions 3 and 6). For two of the six hens (Hens 12.1 and 12.5), however, choice for the low-probability alternative remained flat for Condition 3 whereas choice for this option for one hen (Hen 12.1), decreased and remained below 50% for Condition 4. In Condition 5, previous choice performances for all hens were disrupted, and choice for the left-key remained variable across sessions and subjects.

Results for Conditions 7-11 (Reliability of Stimuli Series)

In this series of conditions, the low-probability alternative was always presented on the left-key using Rd and Gn stimuli, and the non-discriminative alternative was presented on the right-key using Bl and Ye stimuli. The presentation probability for each stimulus in each pair remained the same (i.e., .20 and .80, respectively), as did the overall percentage of reinforcement associated with each alternative (i.e., 20% and 50% reinforcement). With each condition, however, the probability of reinforcement associated with each low-probability stimulus was
altered so that the stimuli that reliably predicted the presence (S+, Rd) and absence (S-, Gn) of 20% reinforcement, was gradually made less reliable across conditions.

As shown in Table 4, the reliability of Rd which previously predicted reinforcement (S+) on the low-probability alternative, was progressively reduced from 100% to 50% reinforcement across conditions (i.e., P(rf) 1.0 to .50, respectively). Similarly, Gn, which previously signalled no reinforcement (S-) on the low-probability alternative, was progressively raised from 0% to 50% reinforcement (i.e., P(rf) 0.0 to .50, respectively). This configuration resulted in a corresponding change to the reinforcement ratio for each low-probability stimulus for each condition, which ranged from 8:0 to 4:4 (S+ : S-/+, or 100% and 0%, to 50% and 50% reinforcement, respectively).

Figure 7 presents the percentage of choice for the low-probability alternative for all subjects for Conditions 7-11. Overall, results for this series of conditions generally show that choice for the low-probability alternative remained relatively exclusive and stable for most subjects across most conditions. When the reliability of the low-probability stimuli was made most unreliable at predicting 20% reinforcement (as in Conditions 10 and 11), choice for this option for two hens (Hens 12.2 and 12.3), became more unstable and progressively decreased across conditions. In contrast, one hen (Hen 12.1) consistently chose the non-discriminative alternative for this series of conditions.

**Condition 7: L-Rd/Gn 7:1 Results.** In Condition 7, the probability of reinforcement associated with each low-probability stimulus (Rd/Gn) was P(rf) .90 and .10, respectively. This corresponded to a reinforcement ratio of 7:1 for each stimulus. The results for Condition 7 are presented in the first panel of Figure 7.
Figure 7. Percentage of choice responses for the low-probability alternative of 20% reinforcement over a higher, non-discriminative alternative of 50% reinforcement, plotted across consecutive sessions for each hen, across Conditions 7-11. The condition labels (e.g., L-Rd/Gn 7:1) along the top of the figure shows the side (L = Left), and paired stimuli associated with the low-probability alternative (Rd/Gn = Red/ Green). The ratios (e.g., 7:1), indicate the reinforcement ratio for each low-probability stimulus (e.g., S+ : S-/+ = Rd/Gn 7:1) for each condition.
Results show that choice for the low-probability alternative was initially variable for all subjects. For example, choice for this option for Hens 12.3 and 12.4 was almost immediate and remained exclusive across sessions. For Hens 12.2, 12.5 and 12.6, however, choice for this option was more gradual. In particular, this group of hens required at least 10 sessions before increases in choice for the low-probability alternative was observed; with higher sessions, choice for this option for all subjects remained relatively high across remaining sessions. For Hen 12.1, however, choice for this option generally decreased, remaining below 50% for this condition.

*Condition 8: L-Rd/Gn 8:0 Results.* In Condition 8, the probability of reinforcement associated with each low-probability stimulus (Rd/Gn) was $P(\text{rf}) = 1.0$ and 0.0, respectively. This corresponded to a reinforcement ratio of 8:0 for each stimulus. Thus, the reliability of the stimuli that differentially predicted the presence ($S^+, \text{Rd}$) and absence ($S^-, \text{Gn}$) of 20% reinforcement on the low-probability alternative was reinstated. The second panel of Figure 7 presents the results for Condition 8.

With the exception of Hen 12.1, results show that when reliable signals that differentially predicted 20% reinforcement on the low-probability alternative were reinstated, there was an immediate and exclusive choice for this option for all hens which remained stable across sessions. Choice for this option for Hen 12.1, however, did not exceed 50%, indicating that this hen consistently chose the non-discriminative alternative associated with 50% reinforcement and unreliable stimuli for this condition.

*Condition 9: L-Rd/Gn 6:2 Results.* In Condition 9, the probability of reinforcement associated with each low-probability stimulus (Rd/Gn) was $P(\text{rf}) = .80$
and .20, respectively. This corresponded to a reinforcement ratio of 6:2 for each stimulus. The results for Condition 9 are presented in the third panel of Figure 7.

Results show that each subject’s choice for the low-probability alternative remained relatively the same as the previous condition except that Hen 12.2 shows a slight decreasing function in choice for this option across sessions.


dition 10: L-Rd/Gn 5:3 Results. In Condition 10, the probability of reinforcement associated with each low-probability stimulus (Rd/Gn) was \( P(rf) .60 \) and .40, respectively. This corresponded to a reinforcement ratio of 5:3 for each stimulus. The fourth panel of Figure 7 presents the results obtained for Condition 10.

Results for Condition 10 show that as the reliability of the low-probability stimuli was made less reliable, choice for this option varied across subjects. For example, choice for the low-probability alternative remained exclusive and stable for three hens (Hens 12.4, 12.5 and 12.6), whereas choice for this option for two hens (Hens 12.2 and 12.3) became more unstable and less exclusive. In particular, fluctuations and a decreasing trend was observed in Hen 12.2’s data set, whereas a progressively decreasing function is evident in Hen 12.3’s data set (e.g., choice performances for this option decreased from 92.5% to 25%). In contrast, choice for the low-probability alternative for Hen 12.1 remained below 50% for Condition 10.

Condition 11: L-Rd/Gn 4:4 Results. In Condition 11, the probability of reinforcement associated with each low-probability stimulus (Rd/Gn) was \( P(rf) .50 \), respectively. This corresponded to a reinforcement ratio of 4:4, for each stimulus. The results for Condition 11 are presented in the last panel of Figure 7.

Results for Condition 11, for all hens, show greater variability in choice for the low-probability alternative across increasing sessions. For example, choice for
this option for Hen 12.5 remained exclusive across sessions, whereas this option became less exclusive and more unstable across higher sessions for Hens 12.4 and 12.6. The results obtained for Hens 12.1 and 12.2 were variable, but remained below 50% choice for this option across sessions. In contrast, fluctuations and a notable decreasing trend was observed in Hen 12.3’s data set (e.g., choice performances for this option decreased from 90% to 37%), where the last 3 sessions remained below 50% choice for this option.

To summarise, Figure 7 shows that initial choice for the low-probability alternative took longer to develop for some hens (Hens 12.2, 12.5 and 12.6) than others (Hens 12.3 and 12.4). With increasing sessions, however, choice for this option became relatively exclusive and stable for most subjects across most conditions. As the reliability of the low-probability stimuli became more unreliable (Conditions 10 and 11), choice for this option remained exclusive for Hen 12.5 across conditions, and less exclusive for Hens 12.4 and 12.6. In contrast, choice for this option for Hens 12.2 and 12.3 was more variable, and a notable decreasing trend was observed in both data sets. For example, choice performances for this option for Hen 12.2 decreased from 92.5% in Condition 10, to 7.5% in Condition 11, whereas choice performance for Hen 12.3 declined from 97.5% to 37.5%, respectively, as well.

Choice for this option for Hen 12.1 remained variable but low, at or below 50%, across this series of conditions, indicating that this hen consistently chose the non-discriminative alternative associated with 50% reinforcement and unreliable stimuli.

**Results for Conditions 12 & 13 (Controls for Bias Series)**

In this series of conditions, the low-probability alternative was always presented on the right-key using Bl and Ye stimuli, and the non-discriminative
alternative was presented on the left-key using Rd and Gn stimuli. The presentation probability for each stimulus in each pair remained the same (as shown in Table 6), as did the overall percentage of reinforcement associated with each alternative (i.e., 20% and 50% reinforcement). Like the previous series of conditions, the reliability of the low-probability stimuli that predicted the presence (S+, Bl) and absence (S-, Ye) of reinforcement was altered from being reliable signals of 20% reinforcement in Condition 12, to being unreliable signals for reinforcement in Condition 13.

As shown in Table 6, the reliability of Bl predicting reinforcement (S+) on the low-probability alternative, was reduced from 100% to 50% reinforcement for each condition (i.e., P(rf) 1.0 to .50, respectively). Similarly, Ye, which would normally predict no reinforcement (S-) on the low-probability alternative, was raised from 0% to 50% reinforcement (i.e., P(rf) 0.0 to .50, respectively). This arrangement resulted in a corresponding change to the reinforcement ratio for each low-probability stimulus (Bl/Ye) for each condition, which was 8:0 in Condition 12, and 4:4 in Condition 13 (S+ : S-/+, or 100% and 0%, to 50% and 50% reinforcement, respectively).

Figure 8 presents the percentage of choice for the low-probability alternative for all subjects across Conditions 11, 12 and 13. Data from Condition 11 was re-plotted in Figure 8 for convenience of comparing each subject’s choice for this option across changing contingencies, and the results are summarised below so that comparisons of choice performance can be drawn across this series of conditions.

Overall, results for this series of conditions show that when the reliability of the low-probability stimuli were made non-discriminative in Conditions 11 and 13, choice for this option for all subjects in Condition 13 was more variable when
Figure 8. Percentage of choice responses for the low-probability alternative of 20% reinforcement over a higher, non-discriminative alternative of 50% reinforcement, plotted across consecutive sessions for each hen, across Conditions 11-13. The condition labels (e.g., L-Rd/Gn 4:4) along the top of the figure shows the side (L = Left, R = Right), and paired stimuli associated with the low-probability alternative (Rd/Gn = Red/Green, Bl/Ye = Blue/Yellow). The ratios (e.g., 4:4), indicate the reinforcement ratio for each low-probability stimulus (e.g., S+ : S-/+ = Rd/Gn 4:4) for each condition.
compared to the results obtained for Condition 11. In contrast, when the reliability of the low-probability stimuli was reinstated in Condition 12, exclusive choice for this option was almost immediate for two hens (Hens 12.2 and 12.3), and gradual for the remaining hens, but with increasing sessions, choice for this option remained relatively high and stable.

**Summary of Condition 11: L-Rd/Gn 4:4 Results.** In Condition 11, the low-probability alternative was presented on the left-key using Rd and Gn stimuli. The probability of reinforcement associated with each low-probability stimulus was $P(rf) = .50$ for each stimulus. This corresponded to a reinforcement ratio of 4:4, respectively. The results for Condition 11 are reproduced in the first panel of Figure 8.

Results for Condition 11, for all hens, show greater variability in choice for the low-probability alternative across increasing sessions. Choice for this option for Hen 12.5 remained exclusive across sessions, whereas this option became less exclusive across higher sessions for Hens 12.4 and 12.6. In contrast, choice for the low-probability alternative for Hens 12.1 and 12.2 remained below 50%, indicating that these hens increasingly chose the non-discriminative alternative during choice-trials. Hen 12.3, however, showed fluctuations with a progressively decreasing trend in choice for this option across sessions, where the last 3 sessions remained below 50% choice.

Visual inspection of the data shows that a short period of hysteresis was clearly evident in the data sets for Hens 12.5 and 12.6, where choice performances on the low-probability alternative became exclusive and stable relatively quickly. Hysteresis was also evident in Hen 12.4’s data set but towards the end of this condition, choice performances for this hen became more unstable. It should be
noted, however, that because the low-probability stimuli were non-discriminative in this condition, their results, in this context, are not indicative of their preference for reliable signals for 20% reinforcement. In contrast, the presence of hysteresis was not as obvious in the remaining data sets. For example, choice performances for Hens 12.1 and 12.2 were consistently low and unstable, whereas Hen 12.3 was still transitioning.

**Condition 12: R-Bl/Ye 8:0 Results.** In Condition 12, the paired stimuli associated with the reinforcement contingencies were reversed. In Condition 12, the low-probability alternative of 20% reinforcement was presented on the right-key using Bl and Ye stimuli, and the non-discriminative alternative of 50% reinforcement was presented on the left-key using Rd and Gn stimuli. The probability of reinforcement associated with each low-probability stimulus (Bl/Ye) was \( P(\text{rf}) = 1.0 \) and 0.0, respectively. This corresponded to a reinforcement ratio of 8:0 for each stimulus. Thus, the reliability of the stimuli that differentially predicted the presence (S+, Bl) and absence (S-, Ye) of 20% reinforcement on the low-probability alternative was reinstated. The second panel of Figure 8 presents the results for Condition 12.

Results show that when reliable signals that differentially predicted 20% reinforcement on the low-probability alternative was reinstated, choice for this option was almost immediate for Hens 12.2 and 12.3 (which remained high across sessions), whereas choice for this option was more gradual for Hens 12.4, 12.5 and 12.6. In particular, the results obtained for Hens 12.4, 12.5 and 12.6 shows a steady increase in choice for the low-probability alternative from Session 5; by Session 10, the hens reached 90% performance on this option and responses continued to remain relatively
high across sessions. In contrast, choice for this option for Hen 12.1 initially oscillated around 50%, before increasing across higher sessions which remained high but unstable.

A short period of hysteresis was evident in the data sets for Hens 12.2 and 12.3, where choice performances on the low-probability alternative became exclusive and stable relatively quickly, indicating a strong preference for reliable signals for 20% reinforcement. In contrast, a longer period of hysteresis was observed in Hens 12.4 and 12.6’s data set where choice performances did not stabilise until Session 7 which indicates a slightly weaker preference for this alternative. Choice performances for the remaining hens had not stabilised by the end of this condition, therefore, hysteresis was not present in their data sets.

*Condition 13: R-Bl/Ye 4:4 Results.* In Condition 13, the probability of reinforcement associated with each low-probability stimulus (Bl/Ye) was $P_{(rf)} .50$, respectively. This corresponded to a reinforcement ratio of 4:4, for each stimulus. The results for Condition 13 are presented in the last panel of Figure 8.

Results for Condition 13, for all hens, show greater variability in choice for the low-probability alternative across increasing sessions. Choice for this option was initially high for all subjects. From Session 4 onwards, however, choice for this option substantially decreased and became flat for Hens 12.4 and 12.5, remaining at or near zero across sessions, whereas choice for this option for Hen 12.3 continued to decrease across this condition, which for the most part, remained below 50%. Choice for this option for Hen 12.6 was exclusive until mid-condition, at which point responding switched to the non-discriminative alternative associated with 50% reinforcement, and then back to the low-probability alternative with increasing
sessions. Choice for this option for Hen 12.1 steadily decreased and generally remained below 50% across sessions. In contrast, choice for the low-probability alternative for Hen 12.2 remained exclusive until mid-condition where choice for this option became more unstable and less exclusive.

Visual examination of the data shows that hysteresis was clearly evident in Hens 12.3 and 12.4’s data set where choice performances stabilised by Session 5. While stabilisation of responses was slightly slower to develop, their results suggest a relatively strong preference for reliable signals for reinforcement. This is because the low-probability stimuli non-differentially signalled 20% reinforcement in this condition and as a result, choice for this option for both hens remained flat across remaining sessions. Hysteresis was also evident in Hen 12.2’s data set but choice performances for this hen became more unstable from mid-condition onwards. In contrast, the remaining hens had not reached a stable state of responses by the end of this condition therefore hysteresis was not detected in their data sets.

To summarise, Figure 8 shows that when the reliability of the low-probability stimuli were made non-discriminative predictors of 20% reinforcement in Conditions 11 and 13, the results obtained for most hens differed considerably between conditions. In particular, if choice for the low-probability alternative was high in Condition 11 (e.g., Hens 12.4, 12.5 and 12.6), choice for this option was low in Condition 13 (see Figure 8). Similarly, if choice for this option was low in Condition 11 (e.g., Hen 12.2), choice for the low-probability alternative was high in Condition 13. Consistent results were obtained for two hens (Hens 12.1 and 12.3) where choice for the low-probability alternative for both hens continued to decrease across Conditions 11 and 13. In contrast, when the reliability of the low-probability stimuli
was reinstated in Condition 12, choice for this option for all hens increased, and remained high and relatively stable across sessions.

Examination of the data sets shows that hysteresis was clearly evident in Hens 12.2 and 12.6’s results in Condition 11, but this did not indicate preference for reliable signals for reinforcement in this context. In contrast, the presence of hysteresis in Hens 12.4 and 12.5’s data sets in Condition 13 indicated a strong preference for reliable signals for reinforcement. In Condition 12, however, hysteresis developed more rapidly for some hens (Hens 12.2 and 12.3) than others (Hens 12.4 and 12.5).
Discussion

Discussion for Replication Series (Conditions 1-6)

In this series of conditions, the paired stimuli and reinforcement contingencies associated with the side keys were repeatedly reversed across Conditions 1-4 and Condition 6 to ensure side and colour biases were ruled out. This arrangement effectively combined Phases 1 and 2 of Stagner and Zentall’s (2010) study, and allowed for a thorough investigation of their findings. Condition 5, however, differed from previous conditions – the occurrence of each stimulus and its corresponding probability of reinforcement was equated at 50%, so that choice performances between the side keys could be assessed, when reliable signals for reinforcement were withheld.

The results from this series of conditions support Stagner and Zentall’s (2010) findings in that most hens consistently demonstrated a strong suboptimal preference for the stimuli that reliably predicted the presence (S+) and absence (S-) of 20% reinforcement, over an alternative associated with unreliable stimuli that non-differentially signalled 50% reinforcement. In addition, choice for this option held for most hens when the stimuli and reinforcement contingencies associated with the side keys was reversed (as in Conditions 2, and 4), and when the paired stimuli associated with the reinforcement contingencies were reversed (as in Conditions 3 and 6). Of note is that choice for the low-probability alternative for most hens was more variable during stimuli reversals than side key reversals. In fact, when the hens had initial experience with the stimuli associated with the low-probability alternative (as in Conditions 1, and 3), choice for this option became almost exclusive for most
hens in fewer sessions in subsequent conditions (see Conditions 2, 4 and 6). In contrast, previous choice performances for all subjects, was disrupted in Condition 5. When the reliability of the low-probability stimuli was reinstated in Condition 6, choice for this option for all subjects returned quite rapidly. Thus, the present results compliment Stagner and Zentall’s findings by effectively demonstrating the reliability and robustness of their results obtained in Phases 1 and 2 of their study (see Figure 6 cf., Phases 1 and 2 of Figure 2).

There were, however, individual differences in choice performances in this series of conditions. Most notable was the results obtained for Hens 12.1 and 12.5 in Condition 3 in which choice for this option for both hens remained at or near zero for this condition. A visual examination of their results obtained in previous conditions (Conditions 1 and 2) show that both hens consistently chose the low-probability alternative, and choice for this option reversed when the stimuli and reinforcement contingencies were reversed in Condition 2. On this basis, a side bias was ruled out and a colour bias was explored.

Given that the low-probability stimuli changed from Rd and Gn in Conditions 1 and 2, to Bl and Ye in Condition 3, it is more than likely that both hens demonstrated a colour bias in Condition 3. It also appears that Hens 12.1 and 12.5 may have required more exposure to the arrangement of the new low-probability stimuli (Bl/Ye) because this colour bias was not evident in their results in Condition 4. If a colour bias had been present in Condition 4, a flat function would have been observed in both data sets – but as shown in Figure 6, this was not the case.

Condition 5 was implemented to assess choice performances between the side keys when reliable signals for reinforcement were withheld. It was expected that the
hens would be indifferent between the alternatives because the reinforcement contingencies in this condition, were equated at 50%. Although the results varied across sessions and subjects, only one hen demonstrated indifference (Hen 12.2). The remaining hens, however, generally demonstrated a right-key bias (Hen 12.1), switching behaviour (Hen 12.3) or a left-key bias (Hens 12.4, 12.5 and 12.6), with indifference developing in higher sessions (Hen 12.6).

It is possible that this left-key bias was caused by a carryover effect from the preceding condition in which Bl and Ye stimuli signalled the low-probability alternative on the right-key. When the stimuli changed to the left-key, it could be that the hens’ choices followed the colours that had previously signalled the low-probability alternative instead of adapting to the new reinforcement contingencies by sampling both keys. Conversely, this bias did not affect the amount of food that could be obtained under this arrangement.

In contrast, it is unclear why Hen 12.1 exhibited a right-key bias in this condition. A preview of this hen’s data set in Conditions 4 and 6 reveal inconsistent choice performances. For example, in Condition 4, choice for the low-probability alternative decreased across sessions, whereas in Condition 6, choice for this option was high and relatively stable. On the basis of these results, colour and side biases were ruled out as possible causative factors for Hen 12.1’s results in Condition 5. It is possible however that the arrangement of Condition 5 may have caused Hen 12.1 to respond differently under the contingencies in effect and therefore, confounded the results obtained for this hen. Generally, however, it can therefore be concluded that on the basis of the results obtained for Condition 5 as a collective, half of the hens remained sensitive to the stimuli that had previously signalled the low-probability
alternative (Hens 12.4, 12.5 and 12.6); one hen came under the control of the contingencies in effect (Hen 12.2); while choice performances for the remaining hens (Hens 12.1 and 12.3) may have come under the control of something other than the arrangement of Condition 5.

With the exception of the results obtained for the hens in Condition 3, it appears that the arrangement of side and colour variability in the present experiment was not a biasing factor in this study. This is supported by Figure 6 which shows that most hens tracked the reliability of the low-probability stimuli that differentially predicted 20% reinforcement as it shifted from one side key to the other (Conditions 2 and 4), and when the colours that signalled this option were altered (Conditions 3 and 6). More importantly, previous choice behaviour was disrupted in Condition 5, but choice for the low-probability alternative returned in Condition 6. The results of this study therefore provide strong evidence that the hens appeared to attend to the signalling value of the stimuli that differentially predicted the presence (S+) and absence (S-) of 20% reinforcement, rather than the global amount of reinforcement that was obtainable (Zentall & Stagner, 2011a). The consequence of this suboptimal choice meant that the hens lost 2.5 times more food that they could have obtained had they chosen optimally, and selected the higher non-discriminative alternative associated with unreliable signals and 50% reinforcement. Thus, the hens demonstrated that they were willing to forego a vast amount of food to obtain reliable signals that differentially predicted a low-probability of reinforcement, and as a result, they simulated human gambling behaviour.

This suboptimal preference for reliable signals for reinforcement, as demonstrated in this study, compliments previous research which showed that rats
(Rivalan et al., 2009; Zeeb et al., 2009) and pigeons (Gipson et al., 2009; Zentall & Stagner, 2011a) were susceptible to choosing suboptimally in choice procedures that simulated human gambling behaviour. In particular, the results of the present study has been replicated many times with pigeons, and many studies reported that their subjects preferred stimuli that differentially predicted a low-probability but high payoff alternative, where the loss of food occurred with greater frequency (i.e., gambling-like alternative), over stimuli that non-differentially signalled a high-probability but low payoff alternative which provided more food overall (i.e., optimal alternative; (Gipson et al., 2009; Laude et al., 2013; Laude et al., 2012; Roper & Zentall, 1999; Stagner et al., 2011; Stagner et al., 2012; Zentall, 2011; Zentall & Stagner, 2011a). The present study therefore adds to the body of research on suboptimal choice, and extends it to a new species – hens.

**Discussion for Reliability of Stimuli Series (Conditions 7-11)**

The aim of this series of conditions was to partially replicate Phase 4 of Stagner and Zentall’s (2010) procedure, and extend their findings. Of particular interest in the present study was the point at which the hens would choose the non-discriminative alternative, when the reliability of the low-probability stimuli was gradually made less reliable over a series of conditions.

The results for this series of conditions show that initial choice for the low-probability alternative took longer to develop for some hens than others. With increasing sessions, however, choice for this option became relatively exclusive, and remained stable for most subjects across most conditions. In fact, choice for this option for two hens was not disrupted until Conditions 10 and 11 (Hens 12.2 and 12.3), whereas one hen (Hen 12.1) consistently chose the non-discriminative
alternative across this series of conditions (see Figure 7). Thus, it appears that the decreasing reliability of the low-probability stimuli did not deter the hens from choosing suboptimally.

In light of the findings from previous research (e.g., Stagner & Zentall, 2010, Part B; Zentall & Stagner 2011a, Experiment 2), it was expected that the hens would demonstrate a strong preference for the non-discriminative alternative if the reliability of the low-probability stimuli was made less reliable. The results for this series of conditions, however, did not support that speculation because choice performances for most hens did not vary as a function of the decreasing reliability of those signals. Subsequently, these results do not extend Phase 4 of Stagner and Zentall’s (2010) findings.

It is logical to consider that the differences between previous research findings and the current results, was due to a procedural artefact in the present study. In particular, unlike previous research, the reliability of the low-probability stimuli was progressively made less reliable across a series of conditions in this study (cf., Stagner & Zentall, 2010, Part B; Zentall & Stagner 2011a, Experiment 2). It is therefore plausible that the gradually decreasing reliability of those signals may have been less salient and less discernible across conditions. In support of this proposition is that all hens received adequate forced-choice trials within sessions to ensure they sampled the reinforcement contingencies associated with each alternative. When the hens were given a choice between those alternatives, however, they continued to choose the suboptimal option despite the decreasing reliability of those signals for 20% reinforcement.
**Discussion for Controls for Bias Series (Conditions 12 & 13)**

The aim of this series of conditions was to rule out side and colour biases by reversing two conditions used in the previous series of conditions. Data from Condition 11 was re-examined in this series of conditions so that comparisons of choice performances could be assessed across changing contingencies. Another aim was to investigate the presence of hysteresis in the data across conditions.

The results from this series of conditions show that when the low-probability stimuli were made non-discriminative in Conditions 11 and 13, choice for the low-probability alternative differed considerably between conditions. Apart from two data sets which remained consistent across these conditions (Hens 12.1 and 12.3), the results indicate that if choice for this option was high in Condition 11, it was low (Hens 12.4 and 12.5) or variable (Hen 12.6) in Condition 13. Similarly, if choice for this option was low in Condition 11, it was high in Condition 13 (Hen 12.2). In contrast, when the reliability of the low-probability stimuli was reinstated in Condition 12, choice for this option was more immediate and exclusive for two hens (Hens 12.2 and 12.3), and gradual for the remaining hens. With increasing sessions, however, choice for this option developed and remained relatively high and stable (see Figure 8).

The results obtained in Condition 12 supports the hypothesis that a suboptimal preference for the low-probability alternative would be observed in this condition and compliments similar findings obtained in Conditions 1-4 and Condition 6 of this study, and previous research. In addition, the speculation that a short transitional period of hysteresis would be observed in this condition, was confirmed by two of the six hens (Hens 12.2 and 12.3), indicating a strong preference for reliable stimuli that
differentially predicted 20% reinforcement. The gradual development of this choice for the remaining hens, however, suggests that perhaps a colour bias or carryover effect occurred from the previous condition, where the low-probability alternative was assigned to the left-key using Rd and Gn stimuli. Alternatively, it could be that prior to learning about the contingencies associated with Condition 12 – which reversed the side key and paired stimuli associated with this option – the hens were somewhat sensitive to the global amount of food that could be obtained from the two alternatives.

The expectation that an optimal preference for the higher probability of 50% reinforcement would be demonstrated in Condition 13 was confirmed by four of the six hens (Hens 12.1, 12.3, 12.4 and 12.6). In addition, a short transitional period of hysteresis was clearly evident in two data sets (Hens 12.4 and 12.5), and more transitory in two others (Hens 12.1 and 12.3). One data set remained unstable across sessions (Hen 12.6), and the last data set (Hen 12.2) disconfirmed this expectation (which may have resulted from a carryover effect).

While hysteresis was confirmed by two data sets (Hens 12.4 and 12.5) in Condition 13, choice for the low-probability alternative did not diminish as rapidly as expected. Indeed, these hens required at least five sessions before choice for this option decreased and became flat. It could be argued, however, that Hens 12.4 and 12.5 required more exposure to the arrangement of this condition before their responses came under the control of the contingencies in effect. Alternatively, a comparison of Phase 4 of Stagner and Zentall’s (2010) results (see Figure 2), and the current findings (Figure 8) show that the decreasing functions in the hens’ data sets were steeper, and stabilised faster than those shown in Figure 2. While it would be
logical to assume that the hens were more sensitive to the contingencies of this arrangement than the pigeons, it is should be noted that Stagner and Zentall pooled data over a series of sessions, and reported the pigeons’ group means choice proportions which could have skewed their data, and masked individual differences. It is therefore quite plausible, that had the hens’ data been collectively pooled, similar results would have been obtained.

In contrast, a comparative analysis of the results obtained in Conditions 11 and 13 led to some interesting speculations. As previously mentioned, the results obtained in Condition 11 could have been confounded by an order effect which might explain why the results did not vary as the reliability of the low-probability stimuli became less reliable in that series of conditions. In Condition 13, however, the results were more variable when compared to Condition 11. When the low-probability stimuli were made non-discriminative in Condition 13, two hens (Hens 12.2 and 12.6) remained sensitive to the stimuli that had previously predicted the presence (S+) and absence (S-) of 20% reinforcement in Condition 12. This finding compliments similar findings obtained in Condition 5 and across Conditions 7-11 in this study. In contrast, four of the six hens became sensitive to the global amount of reinforcement that could be obtained from the alternatives which therefore supports Stagner and Zentall’s (2010) findings in Phase 4 of their study, and previous research (e.g., Zentall & Stagner, 2011a, Experiment 2). An alternative explanation for this finding, however, is that these hens had a history of left-key responding for five conditions (Conditions 7-11) which may have carried over into Condition 13.

For example, in the previous series of conditions the low-probability alternative was assigned to the left-key using Rd and Gn stimuli whereas in
Conditions 12 and 13, this option was assigned to the right-key using Bl and Ye stimuli. The results obtained in Condition 12, rule out any notion of a colour bias in Condition 13. Thus, it is more than likely that these hens did not demonstrate a sensitivity to global reinforcement amounts as previously suggested, but rather, they were exhibiting a left-key bias. It is interesting to note that this left-key bias provided more food overall and was therefore a sensible strategy. More importantly, this left-key bias effectively disrupted their previously habitual suboptimal choice for 20% reinforcement that was so prevalent in this study.

Of particular note, is that the arrangement of Conditions 12 and 13 are comparable to the design of previous research (e.g., Stagner & Zentall, 2010, Part B; Zentall & Stagner 2011a, Experiment 2). In Condition 12, the hens experienced one condition in which the low-probability stimuli were reliable predictors of 20% reinforcement before the stimuli were made non-discriminative in Condition 13. It could therefore be argued that the results obtained in Condition 13, may better reflect choice performances when reliable signals for 20% reinforcement are made non-discriminative, compared to the results obtained in Condition 11.

Finally, because this study was an operant analysis of choice behaviour as opposed to a statistical analysis of the responses obtained, an alternative means of measuring preference for reliable signals for 20% reinforcement was required which meant that visual examinations of the data was conducted to detect the presence of hysteresis. While this technique proved to be a reliable measure of the dependent variable in most cases, there were discrepancies in which the use of this method was flawed (e.g., Hens 12.4, 12.5 and 12.6 in Condition 11, and Hen 12.2 in Condition 13). Given that the low-probability stimuli were non-discriminative in Conditions 11
and 13, the presence of hysteresis in these data sets suggest that something other than the preference for reliable signals was being measured. This is further supported by the procedural design of this experiment in that many contingency changes were implemented simultaneously (e.g., side, colour, two different probabilities of reinforcement). It is therefore quite possible that the existence of hysteresis in these data sets, measured each subject’s preference for 20% reinforcement, over 50% reinforcement, as opposed to their preference for reliable signals. Subsequently, it may be that the technique itself was not flawed, but that there were too many contingency changes within a condition, and that the parameters of the dependent variable it was employed to measure, may have been too narrow.
General Discussion

The purpose of this study was to determine whether animals exclusively choose signals that reliably signal a reinforcing outcome irrespective of the consequences that are associated with those signals. Of particular interest, however, was the signalling value of the stimuli associated with the low-probability alternative, and how choice for this alternative could be affected when the reliability of those signals become less reliable.

The results from this study (Conditions 1-13) demonstrated that most hens consistently chose the low-probability alternative over the non-discriminative alternative, when reliable signals differentially predicted the presence (S+) and absence (S-) of 20% reinforcement (see Figures 6, 7 and 8). In addition, choice for the low-probability alternative for most hens remained almost exclusive across stimuli and side key manipulations of this alternative. When the reliability of the low-probability stimuli was gradually made less reliable across Conditions 7-13, the results revealed that hens do not exclusively choose signals that reliably signal a reinforcing outcome. Indeed, many hens continued to choose suboptimally despite the reliability of those signals becoming less reliable predictors of 20% reinforcement. This was an unexpected finding because it suggests that the signals themselves may be more reinforcing than their subsequent outcome.

Interestingly, forced-choice trials were implemented throughout this study to ensure the hens had adequate experience with both alternatives and their corresponding reinforcement contingencies. But, like human gamblers, it appears that this did not reduce the hens’ frequency of choosing suboptimally, especially
when the signals for 20% reinforcement became less reliable. Not only are present findings contrary to optimal foraging theory and Fantino and Abarca’s (1985) suggestion that an animals’ survival and sensitivity to different food amounts would dictate that they choose optimally, they are also contrary to previous research which demonstrated that preference for the low-probability alternative is only found when discriminative stimuli reliably predict reinforcement (Gipson et al., 2009, Experiment 1; Roper & Zentall, 1999; Stagner & Zentall, 2010, Part A). When reinforcement was not differentially signalled, many studies reported a strong preference for the alternative associated with the higher probability of reinforcement (e.g., Fantino et al., 1979; Gipson et al., Experiment 2; Spetch et al., 1990; Stagner & Zentall, 2010; Part B; Zentall & Stagner, 2011a, Experiment 2). In the present study, only one hen (Hen 12.1) generally chose optimally overall which indicates that this hen was insensitive to the reliable (and unreliable) signals for 20% reinforcement, and more sensitive to the global amount of reinforcement that was obtainable from the alternatives. Generally, however, this study found that the decreasing reliability of the stimuli associated with the low-probability alternative, did not deter many hens from continuing to choose suboptimally. What is not clear, however, is what mechanism was responsible for the hens’ suboptimal choice for reliable (and unreliable) signals for 20% reinforcement.

A plausible mechanism that may have been responsible for the hens’ continued choice for the low-probability alternative may have been the signalling value of the low-probability stimuli. In particular, the present findings could be comparable to that of Zentall and Stagner’s (2011a) account of their results. They proposed that the results obtained in Experiment 2 of their study suggested that the
suboptimal preference found in Experiment 1, was due to the signalling value of the low-probability stimuli (Zentall & Stagner, 2011a). They also explained that the signalling value of these stimuli diminished in Experiment 2 when they were made non-discriminative predictors of reinforcement. In the present study, the hens were exposed to five conditions during Conditions 1-6 in which the low-probability stimuli reliably predicted the presence (S+) and absence (S-) of 20% reinforcement. This exposure may have given the low-probability stimuli added value, and thus they became highly valued. Unlike Zentall’s and Stagner’s account of their findings in Experiment 2 of their study, however, in the present study, it appears that the low-probability stimuli maintained their signalling value in subsequent conditions despite becoming less reliable predictors of the presence and absence of 20% reinforcement.

Consistent with this proposition is that the signalling value of the low-probability stimuli results from conditioned reinforcement principles. Condition reinforcement theory is based on the notion that because the S+ stimulus is paired with food more reliably and immediately than unreliable stimuli, the presentation of the S+ stimulus reinforces behaviour that produces it (Roper & Zentall, 1999). Previous research has also demonstrated that when a stimulus is always associated with 100% reinforcement, it becomes a highly preferred conditioned reinforcer and elicits observing behaviour (Dinsmoor, 1983; Roper & Zentall). Similar predictions about the value of the S+ stimulus were also proposed by Zentall and Stagner (2011a, 2011b) in their certainty of reinforcement hypothesis. In addition, Dinsmoor (1983) proposed that preference for this stimulus increases when the overall probability of reinforcement is low. In the present study, the exposure of the hens to the S+ stimulus on the low-probability alternative during Conditions 1-6 may have elicited
further responding to it in subsequent conditions because initially, this stimulus was associated with food more reliably and immediately than the unreliable signals on the non-discriminative alternative. While this finding is contrary to Dinsmoor’s suggestion that any stimulus that reliably predicts 100% reinforcement would be preferred over other stimuli, it appears that in the present study, previous exposure to an S+ stimulus is also preferred even when it is presented in the absence of reinforcement. This speculation is supported by Figures 6 and 7 where the decreasing reliability of the S+ stimulus that preceded reinforcement on the low-probability alternative, did not deter many hens from choosing suboptimally, even when those signals were non-discriminative (cf., Zentall & Stagner, 2011b). Thus, conditioned reinforcement may have been an alternative mechanism that may have been responsible for the hens’ continued choice for the low-probability alternative.

In addition, the findings of this study also lend support to Zentall and Stagner’s (2011b) notion that it is not necessary for a S+ stimulus to reliably signal reinforcement in order to obtain a strong preference for the low-probability alternative, which was clearly demonstrated by some hens in this study. While this finding is contrary to previous research who found that preference for the low-probability alternative was only demonstrated when stimuli differentially predicted reinforcement (e.g., Gipson et al., 2009; Roper & Zentall, 1999; Stagner & Zentall, 2010), it appears that the strong attractor of the S+ stimulus in this study elicited a very robust behavioural effect and requires further exploration.

An alternative mechanism that may have been responsible for the hens’ continued choice for the low-probability alternative may have resulted from a combination of Pavlovian conditioning, and positive contrast. For example, previous
research demonstrated that the saliency of the S+ stimulus is further enhanced when presented infrequently in the context of the a low-probability of reinforcement, which occurred in this study (Jenkins et al., 1981; Stagner & Zentall, 2010; see also, Fantino, 2001; Gipson et al., 2009; Grace & Hucks, 2013; Roper & Zentall, 1999; Williams, 2002). Consistent with this interpretation is that the positive contrast between the low-probability of 20% reinforcement at the time of choice, and the onset of the S+ stimulus prior to reinforcement, may have given the S+ stimulus additional value (Gipson et al.; Roper & Zentall; Stagner & Zentall, 2010). For example, in the first series of conditions (Condition 1-6) of the present study, 20% reinforcement would have been expected at the time of choice, but the appearance of the S+ stimulus signalled 100% reinforcement. This resulted in an 80% increase from expectation. Of note, however, is that the expectation of reinforcement on this option was also disconfirmed by the S- stimulus on 80% of those trials.

In contrast, an optimal choice of the non-discriminative alternative meant that 50% reinforcement would have been expected at the time of choice, but the appearance of either stimulus associated with this option, did not change that expectation. In light of previous research, this suggests that the appearance of the discriminative stimuli (S+ and S-) enhanced the value of the low-probability alternative (Gipson et al., 2009; Stagner & Zentall, 2010), and in this study, it appears that they continued to do so even when the reliability of those signals decreased across subsequent conditions. For example, the S+ stimulus may have been attributed additional value in the context of its occurrence without food, so that when it did appear, and food followed, the contrast may have been greater because the expectation that food would be absent on this option was already quite high.
In support of this speculation is that some hens continued to choose suboptimally despite the hens being exposed to some choice-trials in which no reinforcement occurred when the S+ was presented. It could be argued, therefore, that because the S+ occurred infrequently, more value was attributed to this stimulus when it preceded food than when food was absent in its presence. This speculation appears counterintuitive because a signal in the presence of no food necessarily is an S- stimulus, therefore, conditioned inhibition should accrue, and suboptimal choice should decrease. But as Stagner et al.’s (2011) study showed, when they manipulated a house-light to make the S- stimulus more salient and less avoidable, they found that each group of pigeons continued to choose suboptimally and that little negative value was attributed to the S- stimulus. Thus, the saliency of the house-light did not deter their pigeons from choosing this option despite the absence of food associated with it (Stagner et al., 2011). Similarly, in the present study, while the gradual decrease in the reliability of the low-probability stimuli may not have been as salient to the hens as perhaps the house-light in the Stagner et al.’s study was, the findings of the present study suggest that little negative value was attributed to the S+ stimulus when it appeared in the absence of food.

Comparable to this proposition also, is delay reduction theory. This theory holds that the saliency of S+ stimulus and thus its strong preference, is derived from its association with a reduction in the delay to reinforcement (Fantino, 1969, 2001). For example, Zentall and Stagner (2011b, Experiment 1) found that if they held the delay to reinforcement on the discriminative alternative constant at 10 s, they could reduce the delay to reinforcement on the non-discriminative alternative from 10 s to 4.37 s, before indifference was observed between the alternatives. This finding
indicated that preference for the reliable stimuli remained strong and were thus, highly valued.

In the present study, the delay to reinforcement on both alternatives were held constant at FT 10-s. The appearance of the S+, in the context of an S- stimulus in the first series of conditions (Conditions 1-6), would have resulted in a large reduction in the delay to reinforcement and therefore may have acquired a better conditioning effect (Singer & Zentall, 2011; Zentall & Stagner, 2011b). In contrast, the unreliable stimuli associated with the non-discriminative alternative, did not reliably signal any reduction in delay to reinforcement, thus their signalling value may have been reduced. In subsequent conditions, however, as the reliability of the S+ was reduced, the S+ stimulus may have been attributed more value, even in the absence of food, because compared to the longer wait on the non-discriminative alternative the S+ stimulus may have continued to signal a reduction in the delay to reinforcement. This is confirmed by the significant finding in this study that the signals themselves may be more reinforcing than their subsequent outcome.

Alternatively, it could be that because of their previous history and extensive experience responding on the suboptimal alternative in the first series of conditions (Conditions 1-6), the hens’ previous investment in this choice maintained suboptimal choice in subsequent conditions. It could therefore be argued that the results obtained in Conditions 7-13, resulted from a sunk cost effect rather than the relative reliability of the stimuli associated with the low-probability alternative (Navarro & Fantino, 2005).

The procedure used in the present study fails to support an information theoretical account of the suboptimal preference demonstrated by the hens.
According to information theory, reducing the probability of reinforcement in this study to 20%, in addition to manipulating the presence and absence of reinforcement (i.e., $P(rf) = .20$ and .80, respectively) on the low-probability alternative so that they were not equally likely, would have reduced the amount of information that this alternative provided (cf., Berlyne, 1957). As a result, this arrangement would have elicited little observing behaviour (Roper & Zentall, 1999; Stagner et al., 2011; Stagner & Zentall, 2010). Thus, a weaker preference for this option should have been found because the expectation of reinforcement was unlikely on this alternative, and was generally not obtained. But as the findings of this study demonstrated, this was not the case which therefore compliments previous research who found similar suboptimal preferences for a low-probability alternative in which information theory could not account for their results (e.g., Roper & Zentall; Stagner & Zentall, 2010; Zentall, 2011).

It remains unclear what theory (or combination of theories) is representative of the suboptimal preference found in this study, or previous studies. It seems more likely, however, that each theory’s contribution to explaining suboptimal choice is dependent upon the procedure used in each study.

The procedures employed in this study demonstrated a sensitive measure of suboptimal choice for reliable (and unreliable) signals for 20% reinforcement. Indeed, many studies outlined above reported an animal’s suboptimal preference for stimuli that reliably predicted less food. Of particular interest, is if future research investigated how reliable those signals must be, before animals begin choosing suboptimally. This could be conducted by reversing the procedures used in Conditions 7-13 of this study. For example, future research could begin with non-
discriminative signals for a low-probability of reinforcement, and gradually increase their reliability over conditions until animals switched to this option. This would make for some very interesting findings.

This study adds to the body of research on suboptimal choice as it demonstrated that animals do not exclusively choose signals that reliably signal a reinforcing outcome. This finding deserves further investigation because it suggests that the signals themselves may be more reinforcing than their subsequent outcomes which may have implications for human gambling behaviours. Namely, that it may not be the ‘win’ in the sense of money in one’s pocket that may be more salient to human gamblers as Breen and Zukerman (1999) pointed out, but rather, the flashing lights, ringing bells and social attention that precedes collecting the money (Madden, Ewan, & Lagorio, 2007; Petry, 2005; Zentall, 2011).
Appendix A

Excel files with a summary of raw data are attached on the accompanying CD.
Appendix B

Hen weights and post-feed amounts during experimentation are attached on the accompanying CD.
Appendix C

Ethics approval (protocol number: 870), is attached on the accompanying CD.
References


doi:10.1038/npp.2009.152


doi:10.1006/lmot.1999.1030


