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Is Social Rank Correlated With Cognitive Ability in Black-capped Chickadees?

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Abstract

Traditionally, dominant animals have been regarded as better competitors in all aspects of life, including cognition. However, the survival and reproductive advantages of being a dominant chickadee are surprisingly modest. It is possible that subordinate individuals compensate for the disadvantages of a lower rank with better cognitive abilities. If dominants are monopolizing prime food sources, subordinates may have developed better associative learning skills by learning to associate novel types of stimuli with food rewards. In this thesis, I asked whether dominance rank is correlated with cognitive ability in Black-capped Chickadees (*Poecile atricapillus*). I determined dominance rank within six flocks of six chickadees, and then tested each bird individually on two different associative learning tasks. I used artificial trees with holes that held food reward in both tasks. The first task was a colour associative learning task, in which birds learned that only holes marked with a specific colour contained a food reward. The second task was a spatial associative learning task, in which birds learned that only holes in specific locations contained a food reward. There were no differences in associative learning or spatial memory between dominant and subordinate birds, showing no support for the hypothesis that there are differences in learning and memory between chickadees of different dominance ranks.

Keywords: associative learning, memory, spatial memory, dominance, social rank, cognitive ability, Black-capped chickadee, *Poecile atricapillus*

Lay Summary

Traditionally, we think of dominant animals as the ones who have the best territories, the most successful offspring, and the best chances of survival. However, evidence suggests that the advantages of being dominant have been exaggerated and that lifetime reproductive success does not differ much between dominant and subordinate animals. This may be because subordinate animals have better learning and memory abilities to make up for the disadvantages of low social rank. I gave Black-capped Chickadees two learning tasks to see if subordinate birds had better learning and memory than dominant birds. In both tasks, birds were presented with trees that had holes drilled into them. Some holes contained sunflower seeds, while others did not. In the first task, birds learned that only holes marked with a specific colour contained sunflower seeds, and in the second task, birds learned that only holes in specific locations contained sunflower seeds. Both dominant and subordinate birds showed equal performance on both learning tasks, showing that learning and memory ability does not differ between chickadees of different rank.

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CHAPTER ONE

General Introduction

Introduction

Dominance hierarchies are common in social animal groups, as they reduce energetically costly confrontations over access to limited resources. The reproductive benefits of being a dominant male can be seen in numerous biological examples. Silverback gorillas (*Gorilla gorilla*) and their troops, Elephant seals (*Mirounga leonina*) and their harems, and Sage grouse (*Centrocercus urophasianus*) with their lekking mating rituals are just a few of the many ways in which dominant males monopolize reproduction in the wild. Traditionally, dominant individuals have been regarded as better competitors not just reproductively, but in all aspects of life, including cognition. As a result, they control access to preferential resources (Smith, 1991), such as food, shelter, and mates. In Black-capped Chickadees (*Poecile atricapillus*), being dominant confers its benefits in both the winter and the breeding season.

In the winter, dominant male chickadees and their partners are more likely to survive until the breeding season than their subordinate counterparts (Desrochers, Hannon & Nordin, 1988; Smith, 1991). There are several reasons for this pattern. First, dominants control access to food by making subordinates wait until they are done feeding (Ficken, Weise & Popp, 1990). Second, dominant chickadees control access to the best foraging locations. Higher ranking chickadees forage in areas of trees that are lower to the ground, closer to the trunks, and have lower risk of predation, forcing subordinate chickadees to forage on the outermost areas of trees where predation risk is highest (Desrochers, 1989). Having control over food and foraging locations is vital in the winter when food is scarce, and daylight is short. Finally, dominant chickadees control access to roosting sites (Desrochers, 1989), and shelter is another crucial factor in surviving the freezing temperatures of North American winters. This combination of advantages contributes to enhanced winter survival of higher-ranking Black-capped Chickadees.

The breeding season confers several other positive benefits that are correlated with dominance. In terms of territory, dominant males are more likely to obtain breeding territories than subordinate males (Desrochers et al., 1988). Furthermore, the territories of dominant males are larger (Smith, 1991). In terms of male songs, dominant males have higher singing rates and have songs that females respond more frequently to in comparison to the songs of subordinate males (Otter, Chruszcz & Ratcliffe, 1997; Hoeschele et al., 2010). When it comes to reproduction itself, dominants have larger clutches, and greater hatching and fledging success than their subordinate counterparts (Otter, Ramsay, & Racliffe, 1999). As a whole, dominants are at an advantage with respect to the factors that enable reproduction, as well as reproduction itself.

Despite the year-round benefits to being dominant, higher-ranking Black-capped Chickadees are not better adapted to the cold than lower-ranking chickadees are. Dominant birds have only slightly better cold acclimatization, as measured by basal metabolic rate, compared to their subordinate counterparts (Lewden, Petit, & Vezina, 2012). Furthermore, dominant and subordinate birds show no difference in summit metabolic rate, a measure of cold endurance (Lewden, Petit, & Vezina, 2012). As mentioned earlier, although dominant chickadees do have a survival advantage over subordinate chickadees, the advantage is not a large one. A model looking at annual survival probability found only a 5.0 to 7.3% benefit of being a high-ranking chickadee (Schubert et al., 2008). Furthermore, although higher dominance ranking corresponds to higher yearly reproductive success, an individual's average rank across its lifespan does not predict its lifetime reproductive success (Schubert et al., 2007). This suggests that the reproductive benefit of being a higher-ranking individual is short-lived when considered across lifetime reproductive output. If there are limited survival and reproductive advantages to

dominance, it is possible that subordinate birds have adapted in other ways that make them similarly successful to dominants in terms of survival and reproduction.

The producer and scrounger dynamic has been well explored in research on the consequences of living in social groups, and is relevant to explaining the surprisingly modest reproductive and survival disadvantages of being a subordinate chickadee. In producer-scrounger systems of foraging, producers are individuals that acquire food by foraging, whereas scroungers are individuals that kleptoparasitize the food acquired by producers (Barnard, 1984). In Mexican Jays (*Aphelocoma wollweberi*), scroungers were found to be dominant to producers, and they were more likely to steal food from others when there were larger differences in dominance rank. Although studies have not directly shown that this pattern holds true in chickadees, a model of the producer-scrounger system suggested that in small foraging groups, such as chickadee flocks, subordinates would play producers, while dominants would play scroungers (Barta & Giraldeau, 1998).

The pattern of dominant scroungers and subordinate producers is important because there is some evidence suggesting that producers are better learners than scroungers. In Zebra finches (*Taeniopygia guttata*), higher levels of scrounging were related to lower foraging efficiency in individuals (Beauchamp, 2006). Better learning ability does not seem to be the only characteristic related to scrounging. In Barnacle geese (*Branta leucopsis*), birds that were more dominant were not just more likely to be scroungers, but more likely to be more neophobic as well (Kurvers et al., 2009). The same pattern in neophobia has been found in chickadees, in which subordinate birds are less neophobic than dominant ones (An et al., 2011). One explanation for this pattern is that subordinates are forced by dominants to forage in novel locations and on novel food types. Subordinate producers may have developed better associative

learning by learning to associate novel stimuli with food rewards. This is supported by the evidence showing that subordinate producers have better learning abilities than dominant scroungers. As such, we can hypothesize that subordinate chickadees may be compensating for the disadvantages of a lower dominance rank through superior cognitive abilities.

Black-capped Chickadees

The Black-capped Chickadee (*Poecile atricapillus*) is a small, overwintering parid that lives across North America. In appearance, the bird has a gray back, wings and tail, white cheeks and underside, a black cap and bib, and buff sides. Although Black-capped Chickadees form social flocks in the winter, their flocks do not persist throughout the year. Flock formation begins in the late summer or early fall, and the flocks are fully formed by early September. Once formed, chickadee flocks are stable and persist throughout the winter. Then, with the approach of breeding season in the spring, the flock breaks up into breeding pairs. Winter flocks are comprised of mated pairs and foreign juveniles, and they consist of three to twelve individual birds. Black-capped Chickadee flocks also have a linear dominance hierarchy, where males are dominant over females, and adults are dominant over juveniles. Although there are some exceptions, mated males and females generally have the same dominance rank in their same-sex groups (Smith, 1976). For example, the alpha male is mated to the alpha female and the beta male to the beta female. Additionally, an individual's rank usually remains stable between years, and rank reversals generally only occur when an individual leaves a flock or dies (Smith, 1976; Schubert et al., 2007).

Their stable dominance hierarchy in conjunction with their caching behavior make Black-capped Chickadees the perfect model system for studying rank and cognitive ability. As non-migratory birds, chickadees have solved the problem of limited food availability and limited

winter daylight hours for foraging by creating food caches when food is abundant and returning

to recover those caches when food is scarce. The ability of Black-capped Chickadees to keep

track of food caches has been attributed at least in part to spatial memory (Krebs et al., 1996;

Sherry, 1984), making these birds the perfect subjects for spatial learning tasks. This, in

conjunction with their dominance hierarchies make chickadees ideal for exploring the idea that

social rank may be associated with cognitive ability, and in the specific case of Black-capped

Chickadees, lower-ranking individuals may develop superior cognitive abilities as a result of

being subordinate.

Social Rank and Cognition

If subordinate chickadees are more reliant on their caches because dominants monopolize

prime food sources, subordinates could be under increased pressure to successfully make and

relocate food caches, resulting in better spatial learning and memory. However, chickadee

studies looking directly at caching and dominance yield a mixture of results. Some studies found

dominant chickadees cached more than subordinate chickadees (Hitchcock & Sherry, 1995;

Pravosudov, Mendoza, & Clayton, 2003), whereas another study found no difference in caching

between dominants and subordinates (Pravosudov & Lucas, 2000). Furthermore, it is important

to note the limitations of observing chickadees caching and recovering, both in a laboratory

environment and in the wild. Laboratory studies report only modest levels of caching (e.g.

Pravosudov et al., 2003; Sherry, 1984), and observational studies of caching in the wild are time

consuming and impractical, suggesting that caching tasks may not be the most efficient way of

measuring spatial learning and memory in Black-capped Chickadees.

More general tests of cognitive ability have been used to examine the relationship

between rank and learning across different species of animals. Male Crab-eating macaques

(*Macaca fascicularis*) tested on a learning set and a reversal task were found to make more errors and take longer to extinguish a reversal task the more dominant they were (Bunnell & Perkins, 1980). On the other hand, Starlings (*Sturnus vulgaris*) that were found to be the fastest learners were also the most socially dominant (Boogert, Reader, & Laland, 2006). Looking specifically at Black-capped Chickadees, results are again varied. One study found that social rank was not related to observational learning ability (An et al., 2011). A second study found that subordinate chickadees cached less food, retrieved caches less efficiently, and performed significantly worse on a chickadee spatial memory task than dominant chickadees did (Pravosudov, Mendoza, & Clayton, 2003).

However, there may be a problem with these previous studies of chickadees in that both used dyads of birds to infer dominance. The first problem with using dyads to evaluate dominance is that they deviate from the natural structure of a flock, which is made up of three to twelve individuals. The second problem is that in dyads, an individual is classified as either a dominant or a subordinate regardless of its rank within a flock. In a dyad consisting of the two most dominant birds in a flock, the lower ranking individual would be incorrectly classified as a subordinate bird. However, this lower ranking individual would be the second most dominant bird within its flock, making it a dominant bird. I therefore determined dominance by simultaneously observing full flocks of six birds.

The Present Study

This study evaluated the relationship between dominance and cognitive ability in chickadees through two different learning tasks. Unlike previous studies that used dyads unrepresentative of natural conditions, I housed chickadees in flocks of six individuals and evaluated their dominance ranking within these flocks. The learning tasks tested both associative

learning and spatial memory, while eliminating the problems related to observing caching

behaviour. The first learning task required birds to associate food reward with a specific colour,

and the second learning task required birds to associate food reward with specific spatial

locations. I predicted better cognitive abilities would allow subordinate chickadees to learn faster

and make fewer memory errors than dominant chickadees in the two learning tasks.

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CHAPTER TWO

Associative Learning in Chickadees

Introduction

Prior research on cognitive abilities across different species has looked at various measures of learning. Several ideas needed to be incorporated into the measure of cognitive ability used in this study. The hypothesis was based on the idea that as producers, subordinate chickadees would have better associative learning than dominant scroungers. Learning to associate novel types of stimuli with food rewards could have facilitated associative learning ability in subordinate producers. As a result, the task required an associative learning component in order to evaluate the relationship between dominance and cognitive ability. A second key component in developing my predictions was the caching behaviour of chickadees. Since dominant chickadees control access to prime food sources, subordinates would have been under increased pressure to rely on their food caches. This pressure may have developed better spatial memory in subordinate chickadees. As such, it was critical to have a spatial memory component in my measures of cognitive ability. Finally, challenges during pilot trials added an additional criterion. The learning tasks used to evaluate cognitive ability had to be representative of the natural behaviour chickadees exhibit in the wild to ensure the task would be completed by all the chickadees being tested. Pilot trials revealed that unnatural learning tasks excluded a subset of chickadees that were unable to complete the task, creating a potential confounding effect. With these three criteria in mind, the measures of cognitive ability used here contained both associative learning and spatial memory components whilst remaining representative of the natural behaviour of Black-capped Chickadees.

In Black-capped Chickadee research, foraging tasks on artificial trees are common. These artificial trees can be set-up in different arrays for a wide variety of experiments examining caching, memory, and learning (e.g. Sherry, 1984; Guitar et al., 2017; Guitar & Sherry, 2018). In

this type of experimental set-up, artificial trees have locations where seeds, mealworms or other types of foods can be cached or recovered. Artificial trees can be created using cut trees, fallen tree branches or wooden doweling. Holes that can hold food rewards are drilled into these materials, and perches can be added underneath these holes using thin wooden doweling where necessary. In these experiments, artificial trees created with wood doweling were used, and they contained sunflower seeds in specific locations. The greatest advantage of using an artificial tree set-up is its similarity to foraging in the wild. This drastically reduces the time the birds need to habituate and learn to use the trees, resulting in increased flexibility in experimental timelines. Using artificial trees to create a type of foraging task for the chickadees fulfilled the requirement for a task representative of natural chickadee behaviour.

Both learning tasks used here were a type of associative learning task. The first learning task was a colour associative learning task, where chickadees learned that one colour showed that a hole was baited with food reward, and a different colour showed that a hole was empty. The second learning task incorporated a spatial memory component into the task. In this task, the cue for food reward was location instead of colour. Through trial and error, each bird learned to go to a unique set of eight holes baited with food reward. A more detailed description is given in the methods section. With these two tasks, all the necessary criteria required for my measures of cognitive ability in Black-capped Chickadees were fulfilled.

The chickadee foraging task on artificial trees is a parallel task to the radial arm maze for rats. Each hole in an artificial tree can be considered as an arm on a radial arm maze. In 1979, Olton and Papas made an important distinction between working and reference memory in a radial arm maze task with rats. In this memory task, one set of arms was always baited, while another set of arms was always empty. Olton and Papas referred to the rats' ability to completely

avoid the empty arms as reference memory, and the rats' ability to avoid revisiting arms they had

already visited as working memory. In the present experiment with chickadees, visits to unbaited

'incorrect' locations were reference memory errors. In the colour associative learning task,

incorrect visits to the colour representing unbaited holes were reference memory errors. In the

spatial associative learning task, incorrect visits to the unbaited holes were considered reference

memory errors. Similarly, revisits to correct but previously emptied holes were considered

working memory errors. The distinction between reference and working memory is important

because the two types of memory are independent of each other (Roberts, Strang & Macpherson,

2015). This distinction would allow me to evaluate any differences in memory performance

between dominants and subordinates that were the result of a difference in reference memory,

working memory, or a combination of the two.

Methods

Chickadee Capture

Chickadees were captured between October, 2016 and February, 2017 at locations within

a 3 km radius from Western University. Forested areas were sought out, and bird feeders filled

with black-oil sunflower seeds were left out so the birds learned to associate the baited areas with

food. Feeders were replenished as needed. Once the feeders had been left out for a minimum of

18 hours, the feeders were temporarily removed, and Potter traps (Figure 2.1) with sunflower

seeds were set up where the feeders had been. A recording of the chickadee fee-bee call was

played from beside the Potter trap to attract nearby chickadees. Once a chickadee landed inside

the Potter trap, it was immediately removed from the trap and put into a cloth bag with a
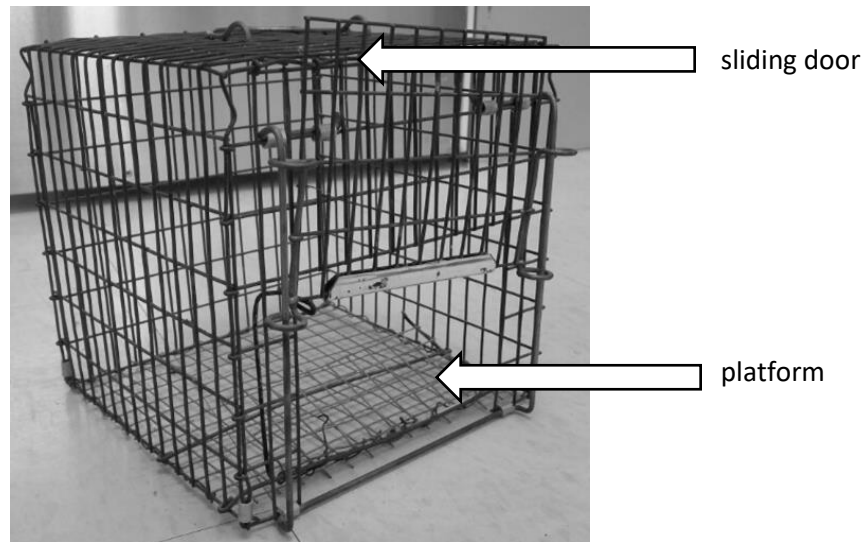
Figure 2.1. A Potter Trap. When a bird lands on the platform, the sliding door moves downwards, trapping the bird inside the trap.

drawstring for transportation. The Potter trap was then reset. Birds spent a maximum of 40

minutes in the cloth bags. Once the chickadees were transported to AFAR, they were weighed

and banded, placed into individual cages, and habituated to the experimental room as described

below.

Chickadee Identification

For identification, colour bands were placed on chickadees' legs. Up to two colour bands

were put on each leg and these bands were noted using abbreviations for each colour as shown in

Table 2.1. The colour bands on the right leg were listed first from top to bottom, followed by the

colour bands on the left leg from top to bottom. For example, a bird with an orange colour band

on the right leg, and a yellow band on top of a white band on the left leg would be noted as

org/ylw,wh.

Chickadee Housing

Once this was completed, chickadees were released into an outdoor aviary. Each aviary housed a

flock of six chickadees, and the flocks remained in these outdoor aviaries for the duration of the

experiment. Chickadees had ad libitum access to a mixture of sunflower seeds and Mazuri®

Small Bird Maintenance Diet ground together, as well as whole sunflower seeds and water.

Water was kept on a heated plate so it would not freeze. Since chickadees were not always

caught on the same day in groups of six, experimentation did not commence until an aviary had

held a group of six chickadees for 48 hours. This ensured that the group of six chickadees would

establish a dominance hierarchy and form a flock before the experiment started. Although there

is no published data on how rapidly dominance hierarchies form in chickadee flocks, wild

chickadee flocks exhibit stable dominance interactions that persist throughout the winter (Smith,

Table 2.1. Abbreviations used to denote colour bands.

Band Colour	Abbreviation
Brown	Brn
Black	Blk
White	Wh
Green	Grn
Red	Rd
Dark Blue	Blu
Sky Blue	Sky
Yellow	Ylw
Orange	Org
Grey	Gry

1976). Accordingly, dominance interactions between individual birds in this experiment did not change over time, showing that 48 hours was sufficient in establishing a stable hierarchy within the experimental flocks.

Daily Trials

Chickadees were brought inside from the outdoor aviaries between 8-10 AM daily for testing. Once inside, chickadees were placed in individual cages in a holding room, where they could see and hear, but not physically interact with each other. Dominance assessments and associative learning tasks were conducted daily, with the order alternating between days. On the first day, chickadees were given a habituation phase. This was followed by four days of the colour associative learning task. On the sixth day, chickadees were given a second habituation phase, followed by four days of the spatial associative learning task. Habituation and learning trials were conducted twice daily, with one dominance assessment per day. Trials were conducted for ten days, for a total of eight of each type of learning trial, one habituation phase prior to the start of each type of learning trial, and a total of ten dominance assessments.

Room set-up. The experimental rooms consisted of a holding room, free-flight room, and an observation room. The holding room had a series of platforms where individual cages could rest, and behind each cage was a door leading into the free-flight room. This door could be remotely opened from the observation room, allowing chickadees to fly between the free-flight room and their individual cages without being handled. This minimized stress for the birds during testing. The free-flight room was connected to the observation room by a door, so the observer could freely move between the rooms. A one-way mirror allowed for behavioral observations, while preventing the observer from being seen by the chickadees.

Dominance assessment. A dominance platform was set up right in front of the two-way mirror in the free-flight room so the colour bands of individual birds could be seen with the naked eye. The dominance platform consisted of a flat surface containing food and water. Perches were also set up around the room. The winner and loser of each aggressive interaction were recorded in a dominance matrix. The types of behaviours used to assess dominance are shown in an ethogram in Table 2.2. The total number of winning interactions an individual had was divided by the total number of aggressive interactions an individual participated in to calculate the percentage of wins for each individual. The percentage of wins was then ranked in order from highest to lowest, ranking birds from most dominant to most subordinate (Figure 2.2). Dominance trials were conducted daily to obtain an accurate running record of dominance ranks. Birds were also group-housed in the experimental flocks between daily trials to maintain dominance relations.

Habituation.   During the habituation phases, six artificial trees with eight holes each were set up in random locations around the free-flight room. Each hole contained a small piece of sunflower seed and had a Post-it® note stuck beside it to make the location of the hole apparent. Birds have sophisticated colour vision (Martin & Osorio, 2008), so locating and distinguishing different coloured Post-it® notes would not have been challenging for the chickadees. Birds were let into the room individually and allowed to search the trees for ten minutes. If a bird had not started searching in the first five minutes of the trial, the trial was extended for an additional five minutes, for a 15-minute session. If the bird still had not started searching at the ten-minute mark, the trial was extended to a 20-minute session. Two habituation trials were run in each habituation phase. Habituation trials were run immediately following bird capture. If birds did not start searching by the end of two habituation trials, these birds were not

Table 2.2. Ethogram of behaviours used to assess dominance.

Behaviour	Description
Waiting	Waiting for another chickadee to finish feeding or drinking
Supplant	Displacing another chickadee
Retain	Maintaining position when another chickadee attempts to supplant
Lunge	Thrusting beak at an opponent

		WINNER					
		Rd / Sky,Wh	*Org/ Wh,Blu*	*Sky,Blu / Grn*	*Brn / Wh,Wh*	*Ylw/ Grn,Grn*	*Blu,Rd/ Blu*	**Total Losses**
LOSER	*Rd / Sky,Wh*	50% Rank 4	R		R W	W		4
	Org/ Wh,Blu		64.7% Rank 1	LR R R		R W R		6
	Sky,Blu / Grn		W	62.5% Rank 2		W S		3
	Brn / Wh,Wh	R R	R R W S	R R	26.7% Rank 5	W S L		11
	Ylw/ Grn,Grn	W L	W R R R S		W	52.9% Rank 3		8
	Blu,Rd/ Blu				S		0% Rank 6	1
	Total Wins	4	11	5	4	9	0	% Won

Figure 2.2. Example of a daily dominance matrix for one flock. Each letter in the white boxes represents a behaviour: L = Lunge, R = Retain, S = Supplant, W = Waiting. These behaviours are pairwise dominance interactions between a winner, outlined in italics in the top row, and a loser, outlined in italics in the left column. The abbreviations used to denote the colour bands for identifying birds can be found in Table 2.1. The wins for each bird are shown in the columns, with the total number of wins for each bird shown in the light

grey boxes along the bottom row. The losses for each bird are shown in the rows, with the total number of losses shown in the dark grey boxes in the right-most column. Each bird's percentage of wins across all its interactions, and its resulting rank is shown in the black boxes going diagonally across the matrix.

used in the experiment. In order to facilitate behavioral observations, each tree was labelled with

a letter from A to F and the holes on each tree were labelled with a number from 1 to 8.

Colour associative learning task. As in the habituation phase, six artificial trees with

eight holes each were set up in random locations around the free-flight room. However, only one

of the six trees were baited with sunflower seeds. The holes of the baited tree had different

coloured Post-it® notes than the rest of the trees (e.g. baited tree was blue, while the rest of the

trees were pink; Figure 2.3). The birds had to learn to associate the unique Post-it® note colour

with the food reward. The specific tree that was baited changed between trials, but the colours of

the Post-it® notes indicating the presence or absence of food remained constant. Trials ran until

the bird recovered all eight seeds, or ten minutes had elapsed. The task was run for eight trials

over the course of four days. Dominance trials were held in the same room, but required a

different set-up, so the location of the trees were marked with tape to ensure that the orientation

and location of the trees remained constant between trials when the trees were moved in and out

of the room.

Spatial associative learning task.   In this task, the associative learning cue was spatial

location, rather than colour. Six artificial trees with eight holes each were set up in random

locations around the free-flight room. In this task, all of the holes had identically coloured Post-

it® notes. Each bird was pseudo-randomly assigned 8 specific holes that would be baited (Figure

2.4). These holes remained constant between trials, but were different for each bird. The birds

had to learn to associate food reward with these specific locations through trial and error. Trials

ran until the bird recovered all eight seeds, or ten minutes had elapsed. The task was run for eight

trials over the course of four days. As the trees were moved in and out of the room daily due to

the dominance trials, the location of the trees were marked with tape to ensure that the
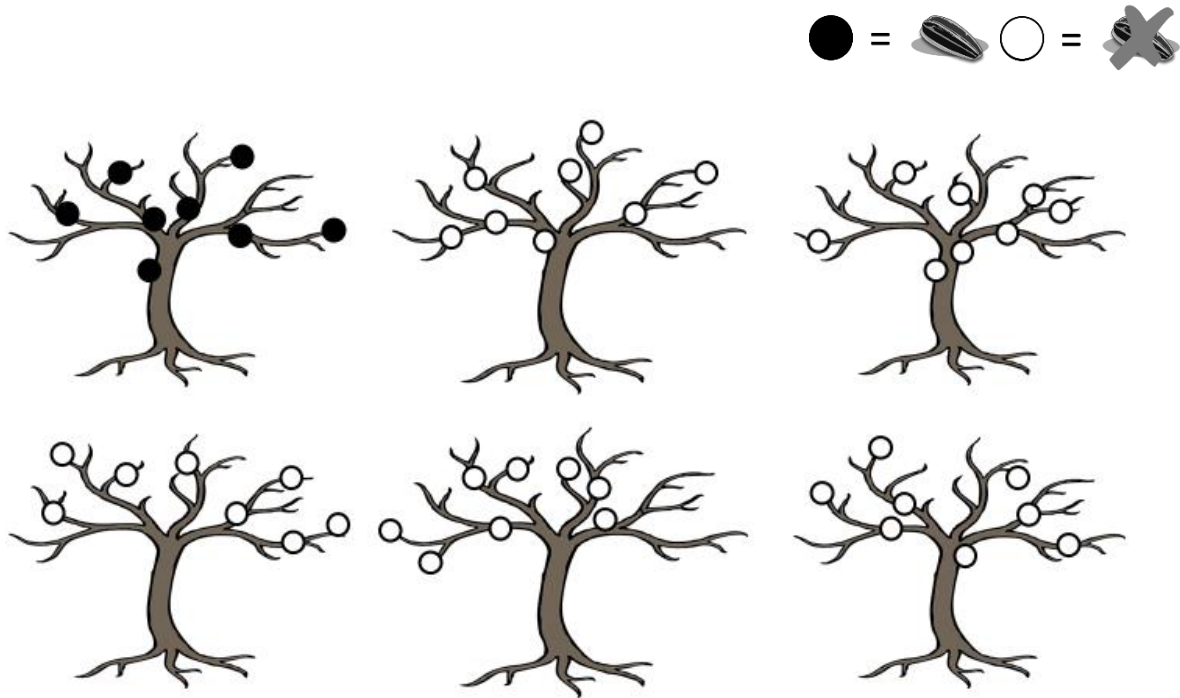
Figure 2.3. The colour associative learning task. Black dots represent holes baited with seeds, and white dots represent empty holes. On each trial, the tree with baited holes was switched. The baited holes had different colour Post-it® notes than the rest of the trees, so the birds had to learn a colour association to solve the task.
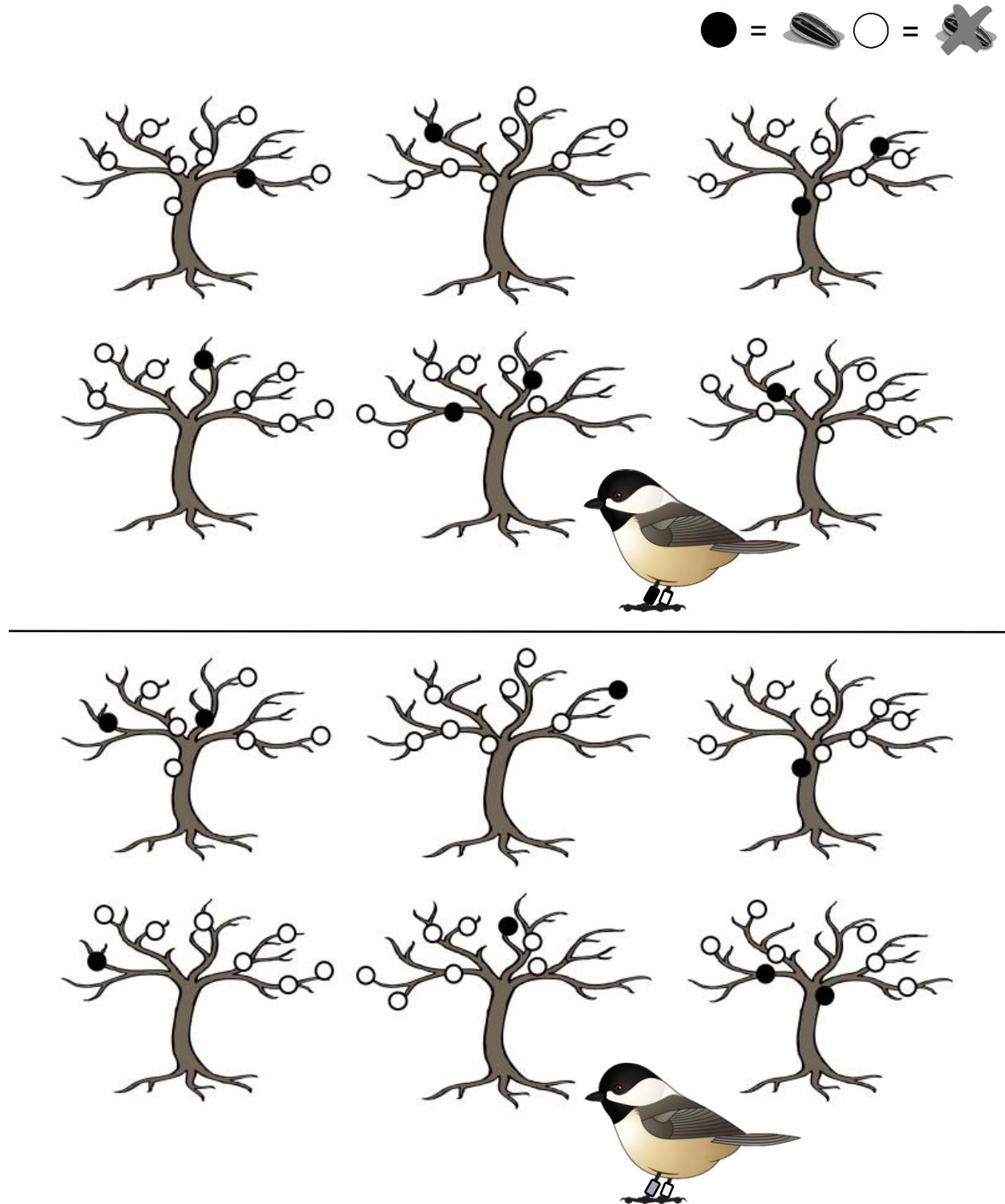
Figure 2.4. The spatial associative learning task. Black dots represent holes baited with seeds, and white dots represent empty holes. As shown above, each bird had a unique set of baited holes that remained the same across trials (Bird Black/White in upper panel, bird Grey/White in

lower panel). This was a spatial association task because birds had to learn the locations of the baited holes through trial and error and then remember them.

orientation and location of the trees remained constant between trials.

Observations. Behavioral observations were initially taken by hand. Trial duration, seed removal, and the holes that each bird chose to visit were recorded. However, partway through the fourth flock and continuing to the end of the experiment, observations were recorded with Noldus Observer software. This was an easier method of data collection, and gave each observation a timestamp, which allowed further analyses of the chickadees' behaviour.

Chickadee Sexing

Chickadee blood samples were collected by pricking the ulnar vein with a needle to form a blood droplet that was then collected with a capillary tube. Between half to a full tube of blood was collected for each bird. The blood in the capillary tube was immediately put onto filter paper by placing one end of the capillary tube on the filter paper, and then allowing the blood to drain out. Blood was spread onto the filter paper in a concentrated circle, then a drop of ethylenediaminetetraacetic acid (EDTA) was placed on top of the blood for preservation. The sample was given time to dry, then placed in a plastic ziplock bag for storage with a double layer of paper towel separating the samples to prevent cross-contamination. DNA was extracted from the collected blood samples. Then, P2 and P8 primers were used to amplify a homologous intron in the CHD-W and the CHD-Z genes, which are the sex genes in Black-capped chickadees. The lengths of the CHD genes differ in almost all birds, so an agarose gel electrophoresis will show one band in males and two bands in females, allowing for sex determination (Griffiths, Double, Orr, & Dawson, 1998; Figure 2.5). The DNA of each bird was pipetted into separate wells in an agarose gel, and electrophoresed. The resulting band pattern was used to determine the sex of each bird (Figure 2.5).
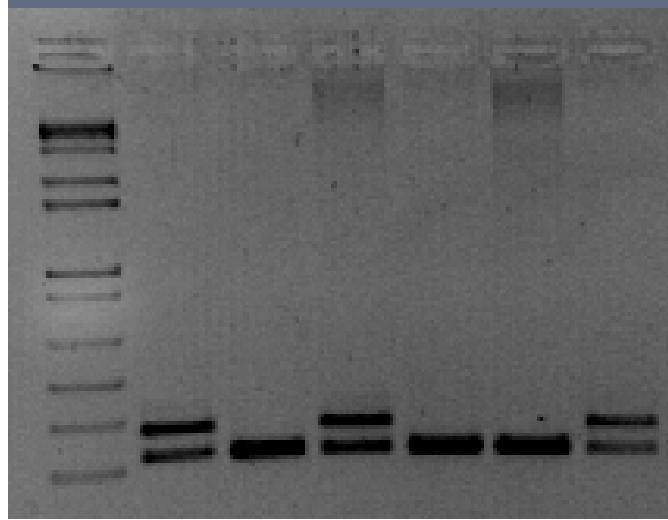
Figure 2.5. DNA chickadee sex identification using PCR with P2 and P8 primers. The first

vertical column contains a DNA ladder marking different base-pair sizes. Each column thereafter

contains the DNA of an individual bird. In birds, females have the CHD-Z and CHD-W

chromosomes, while males have two CHD-Z chromosomes. Therefore, the double banded

columns indicate a female, and the thicker single banded columns indicate a male.

Statistical Analyses

Five variables from each of the two learning tasks were assessed using a repeated measures ANOVA with trial as a within-subjects factor with eight levels, and rank as a between-subjects factor with six levels. Trial was an important within-subjects factor for evaluating learning, and evaluating rank would reveal any differences in cognitive abilities between dominant and subordinate birds. Exploratory analyses were conducted for flock membership and sex. The effect of flock was examined in a separate repeated measures ANOVA with flock as the between-subjects factor with six levels, and trial as a within-subjects factor with eight levels. The effect of sex was also assessed in a separate repeated measures ANOVA with sex as the between-subjects factor with two levels, and trial as a within-subjects factor with eight levels. A combined ANOVA testing all four factors could not be conducted because the sample size was insufficient for a single test. All statistical analyses were conducted using IBM® SPSS® Statistics software.

Results

Colour Associative Learning Task

The variable 'revisits' was the number of times a bird returned to a location that had originally been baited. Birds always recovered seeds on their first visit to a baited location, so any following visits were revisits to a previously emptied location. The number of revisits was calculated by counting the total number of times birds visited baited locations, then subtracting the number of times seeds had been recovered from those locations. There was no significant effect of rank on revisits ($F(5, 29) = 0.91$, $p = .49$, $\eta_p^2 = .14$), but there was a significant effect of trial ($F(7, 203) = 4.27$, $p < .001$, $\eta_p^2 = .13$; figure 2.6a). Post-hoc Bonferroni pairwise

a) Mean Revisits by Rank

b) Mean Proportion of Correct Searches by Rank

c) Mean Number Correct in First Eight Searches by Rank

d) Mean Total Number of Seeds Recovered by Rank
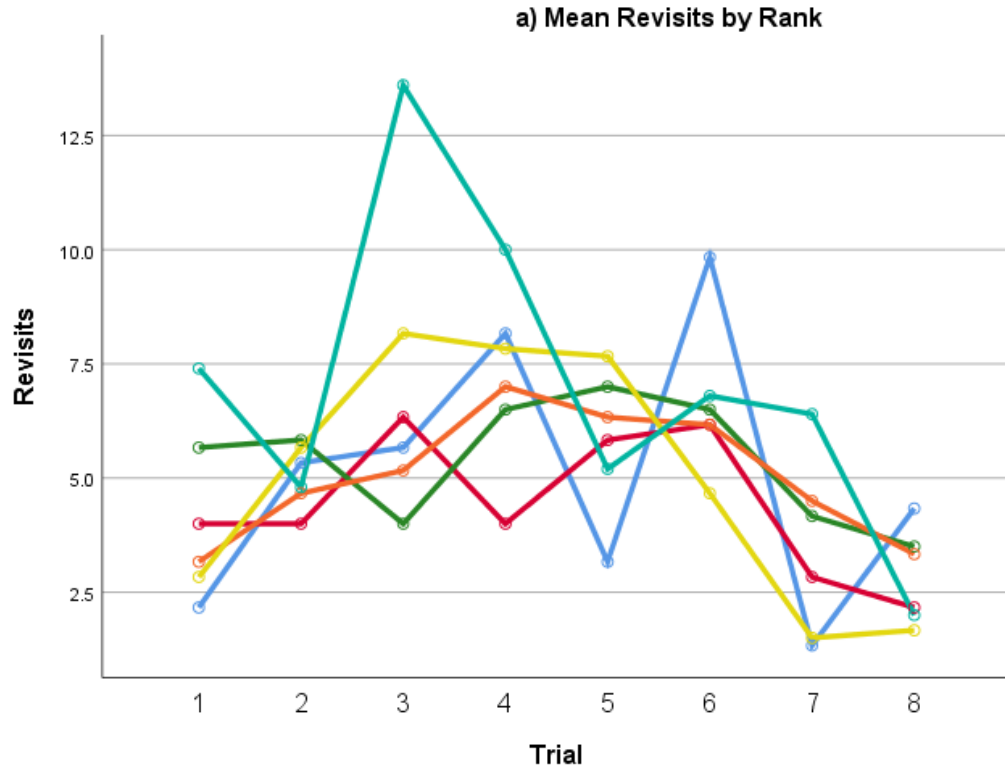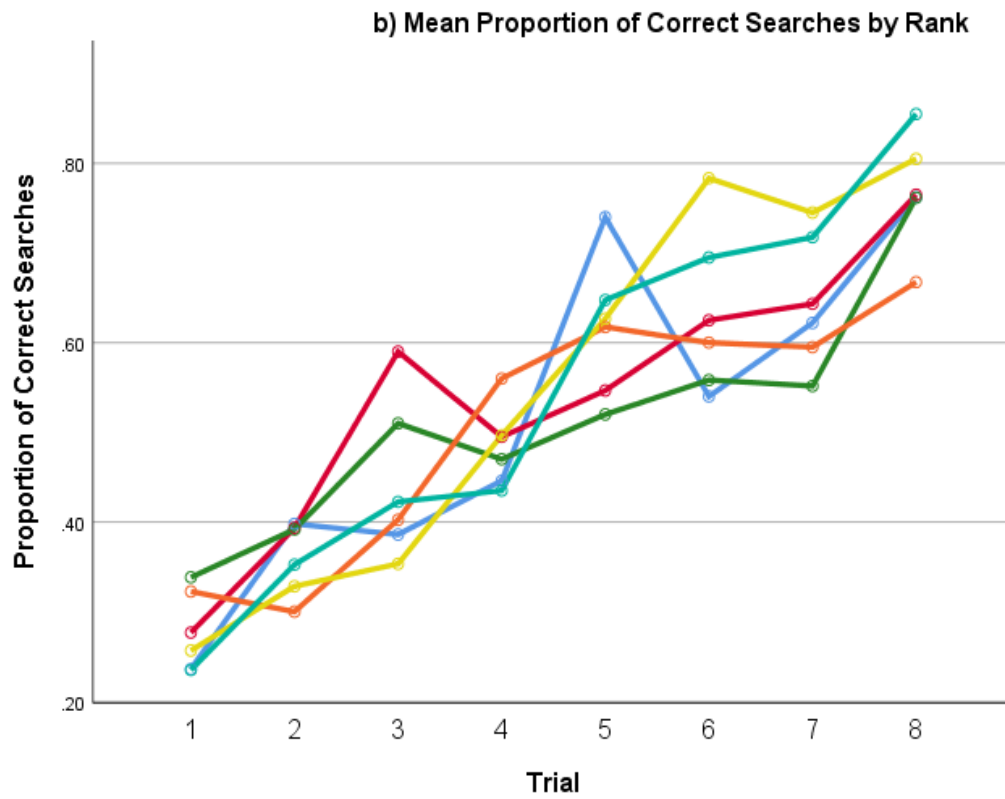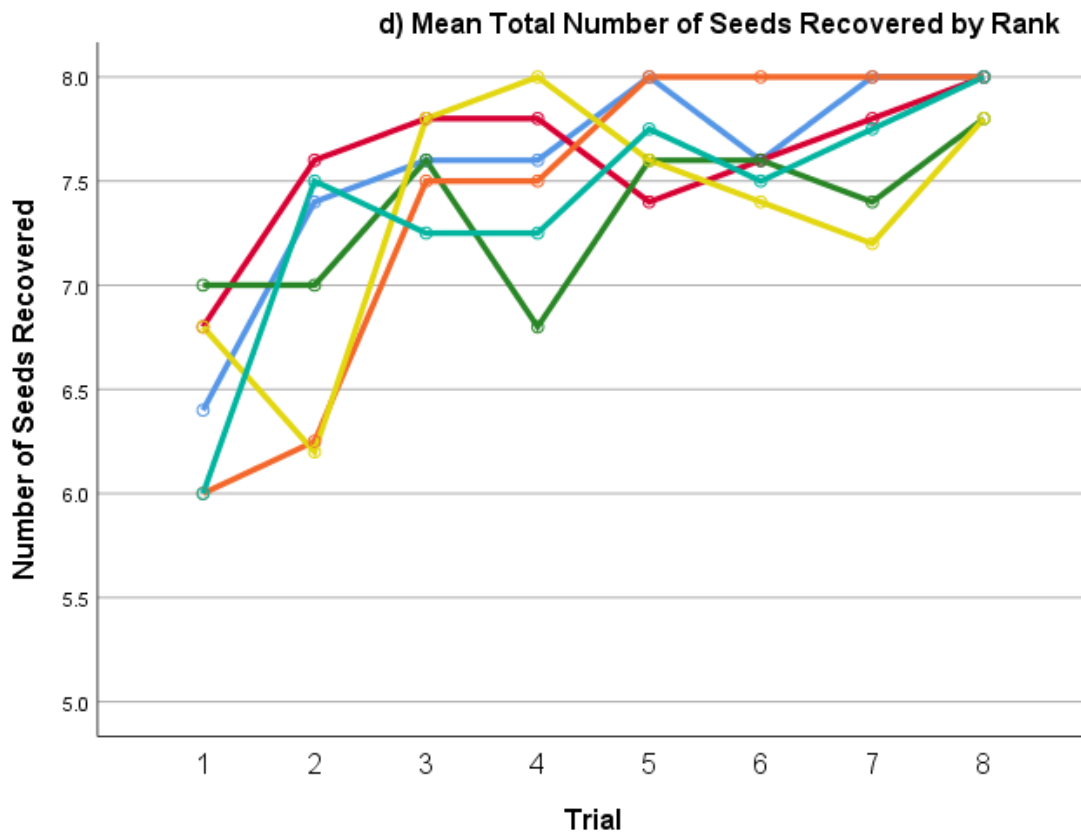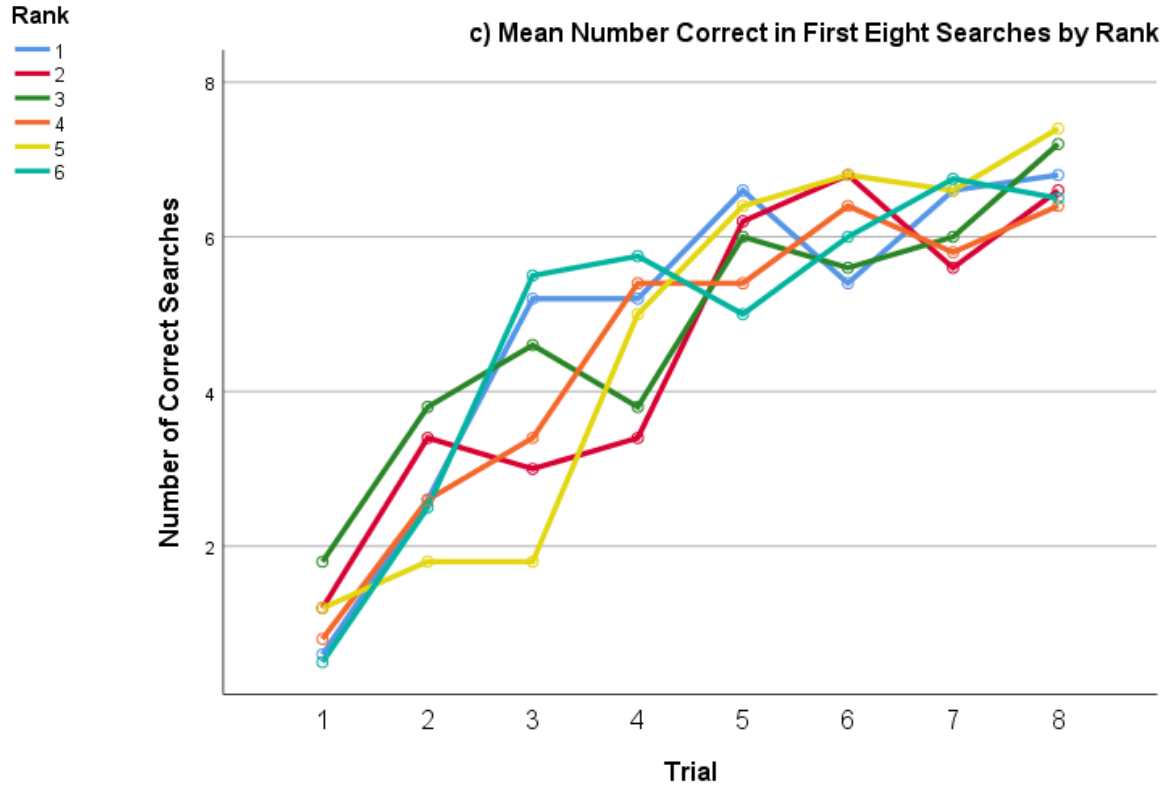
Figure 2.6. Colour Associative Learning Task. a) Mean Revisits by Rank b) Mean Proportion of Correct Searches by Rank c) Mean Number Correct in First Eight Searches by Rank d) Mean Total Number of Seeds Recovered by Rank e) Mean Seeds Recovered in First Eight Searches by Rank.

comparisons show that the mean number of revisits on trial 8 was lower than on trials 3, 4 and 6

(Appendix A, Table A1). There was no interaction between rank and trial on revisits ($F(35, 203)$

$= 0.82$, $p = .75$, $\eta_p^2 = .12$). Sex did not have a significant effect on revisits ($F(1, 27) = 1.89$, p

$= .18$, $\eta_p^2 = .066$). The effect of flock on revisits was significant ($F(5, 29) = 2.49$, $p = .05$, η_p^2

$= .30$), but post-hoc analyses using Tukey's HSD indicated there were no significant pairwise

differences between flocks (Appendix A, Table A2).

The variable 'proportion of correct searches' was the number of times an individual bird

searched correct, i.e. baited, locations as a proportion of visits to all locations. For this variable,

any revisits to previously baited locations were still considered correct searches. The proportion

of correct searches was calculated as the number of correct searches to baited locations a bird

made, divided by the total number of searches a bird made. There was no significant effect of

rank on the proportion of correct searches birds made ($F(5, 25) = 0.19$, $p = .96$, $\eta_p^2 = .037$), but

there was a significant effect of trial ($F(7, 175) = 24.3$, $p < .001$, $\eta_p^2 = .49$; figure 2.6b). In

general, the proportion of correct searches increased across trials (post-hoc Bonferroni pairwise

comparisons in Appendix B, Table B1). There was no interaction between rank and trial on the

proportion of correct searches birds made ($F(35,175) = .77$, $p = .81$, $\eta_p^2 = .13$). Sex ($F(1, 23) =$

1.82, $p = .19$, $\eta_p^2 = .073$) did not have a significant effect on proportion of correct searches. The

effect of flock on proportion of correct searches was significant ($F(5, 25) = 4.05$, $p = .008$, η_p^2

$= .45$), and post-hoc analyses using Tukey's HSD indicated that flock four had a significantly

higher proportion of correct searches than flocks one ($p = .023$), two ($p = .044$), and six ($p = .039$)

(pairwise comparisons in Appendix B, Table B2).

The variable 'number correct in first eight searches' was the number of visits to correct,

baited locations each bird made in its first eight searches. This variable was calculated by

counting the number of times birds went to correct locations in their first eight searches. For this

variable, any revisits to previously baited locations were still considered correct searches. There

was no significant effect of rank on the number correct in first eight searches ($F(5, 23) = 0.22$, p

$= .95$, $\eta_p^2 = .045$), but there was a significant effect of trial ($F(7, 161) = 40.3$, $p < .001$, $\eta_p^2 = .62$;

figure 2.6c). In general, the number of correct searches in the first eight searches increased

across trials (post-hoc Bonferroni pairwise comparisons in Appendix C, Table C1). There was no

interaction between rank and trial on the number correct in first eight searches ($F(35, 161) = 1.08$,

$p = .36$, $\eta_p^2 = .19$). Sex did not have a significant effect on the number correct in first eight

searches ($F(1, 22) \approx 0.000$, $p = 1.00$, $\eta_p^2 \approx .000$). The effect of flock on number correct in first

eight searches was significant ($F(5, 23) = 5.85$, $p = .002$, $\eta_p^2 = .49$), and post-hoc analyses using

Tukey's HSD indicated that flock five had a higher number correct in first eight searches than

flocks one ($p = .005$), two ($p = .008$), and three ($p = .028$) (pairwise comparisons in Appendix C,

Table C2).

The variable 'total number of seeds recovered' was the total number of seeds each bird

found in a given trial. Mauchly's test indicated that the assumption of sphericity had been

violated ($\chi^2(27) = 135$, $p < .001$), so degrees of freedom were corrected using Greenhouse-

Geisser estimates of sphericity ($\varepsilon = 0.35$). There was no significant effect of rank on total

number of seeds recovered ($F(5, 22) = 0.14$, $p = .98$, $\eta_p^2 = .031$), but there was a significant

effect of trial ($F(2.46, 54.1) = 6.7$, $p = .001$, $\eta_p^2 = .23$; figure 2.6d). Number of seeds recovered

generally increased across trials up to its maximum possible value of 8 seeds (post-hoc

Bonferroni pairwise comparisons in Appendix D, Table D1). There was no interaction between

rank and trial on total number of seeds recovered ($F(12.3, 54.1) = 0.67$, $p = .78$, $\eta_p^2 = .13$). Sex

($F(1, 21) = 0.90$, $p = .62$, $\eta_p^2 = .012$) and flock membership ($F(4, 23) = 0.57$, $p = .69$, $\eta_p^2 = .090$) did not have significant effects on total number of seeds recovered.

Finally, the variable 'seeds recovered in first eight searches' was the number of seeds recovered by each bird in the first eight searches it made in a given trial. There was no significant effect of rank on seeds recovered in first eight searches ($F(5, 23) = 0.30$, $p = .91$, $\eta_p^2 = .062$), but there was a significant effect of trial ($F(7, 161) = 36.6$, $p < .001$, $\eta_p^2 = .61$; figure 2.6e). Seeds recovered in the first eight searches generally increased across trials (post-hoc Bonferroni pairwise comparisons in Appendix E, Table E1). There was no interaction between rank and trial on seeds recovered in the first eight searches $F(35, 161) = 0.95$, $p = .55$, $\eta_p^2 = .17$. Sex ($F(1, 22) = 0.16$, $p = .69$, $\eta_p^2 = .007$) did not have a significant effect on seeds recovered in first eight searches. There was a significant effect of flock membership on seeds recovered in first eight searches ($F(4, 24) = 5.73$, $p = .002$, $\eta_p^2 = .49$), and post-hoc analyses using Tukey's HSD indicated that flock five had more seeds recovered in first eight searches than flocks one ($p = .003$), two ($p = .005$), and three ($p = .045$) (pairwise comparisons in Appendix E, Table E2).

Spatial Associative Learning Task

The variables in the spatial associative learning task were calculated identically to the variables in the colour associative learning task. For the variable 'revisits', Mauchly's test indicated that the assumption of sphericity had been violated ($\chi^2(27) = 78.2$, $p < .001$), so degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity ($\varepsilon = 0.54$). There was no significant effect of rank ($F(5, 29) = 0.67$, $p = .65$, $\eta_p^2 = .10$) or trial ($F(3.8, 110) = 2.39$, $p = .058$, $\eta_p^2 = .076$; figure 2.7a). There was no interaction between rank and trial on revisits ($F(19.0, 110) = 0.67$, $p = .84$, $\eta_p^2 = .10$). Sex did not have a significant effect on revisits ($F(1, 27) = 2.81$, $p = .11$, $\eta_p^2 = .094$). Flock had a significant effect on revisits ($F(5, 29) = 259$, $p < .001$,

Rank
— 1
— 2
— 3
— 4
— 5
— 6

a) Mean Revisits by Rank

Revisits

Trial

b) Mean Proportion of Correct Searches by Rank
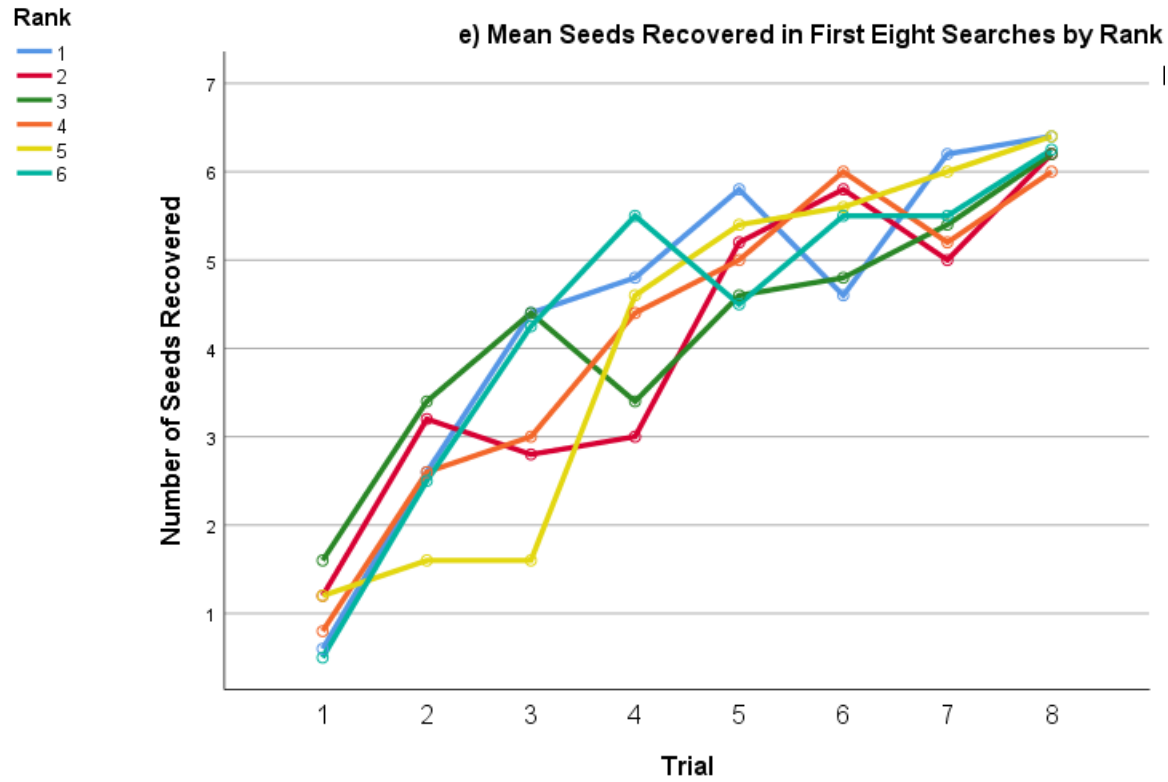
Proportion of Correct Searches

Trial
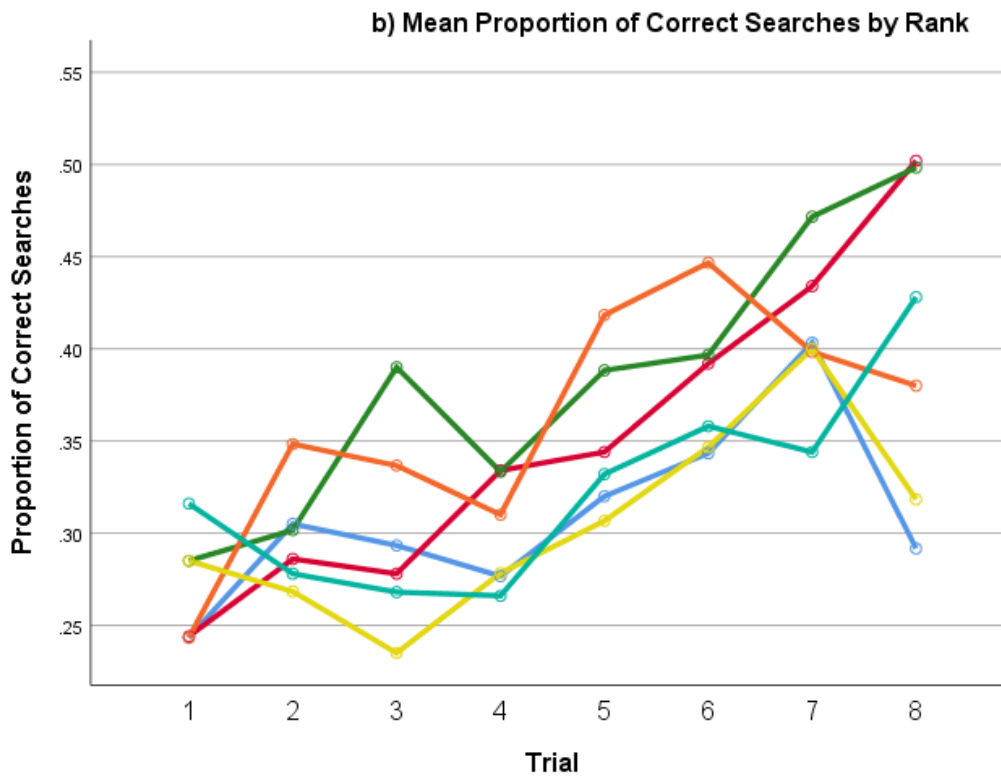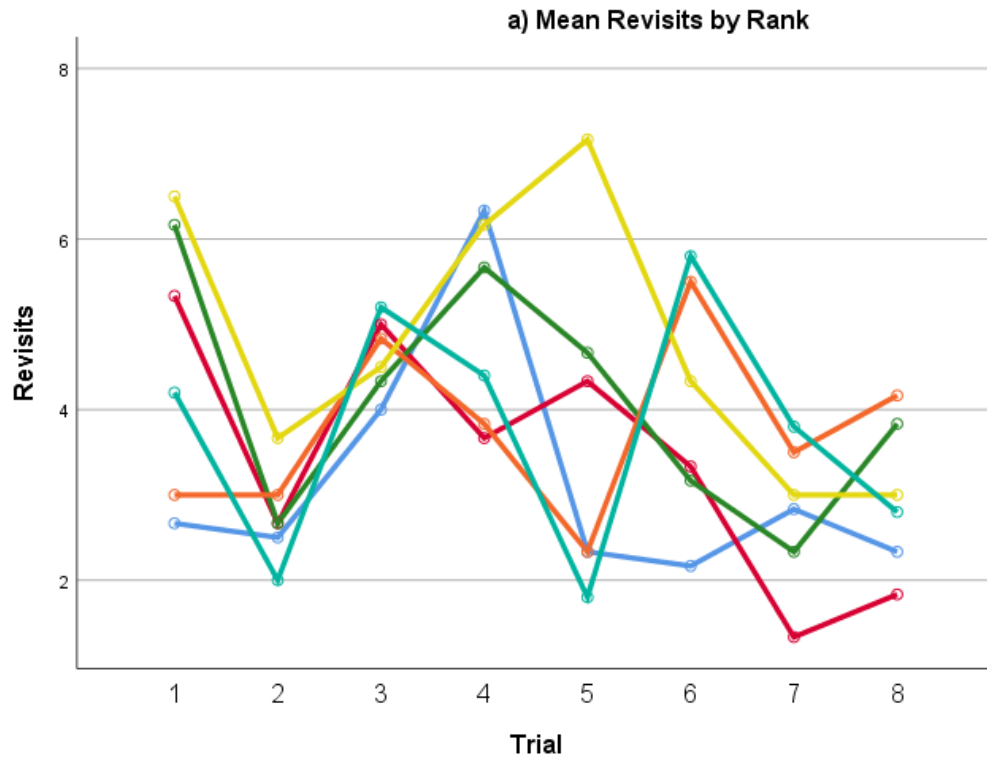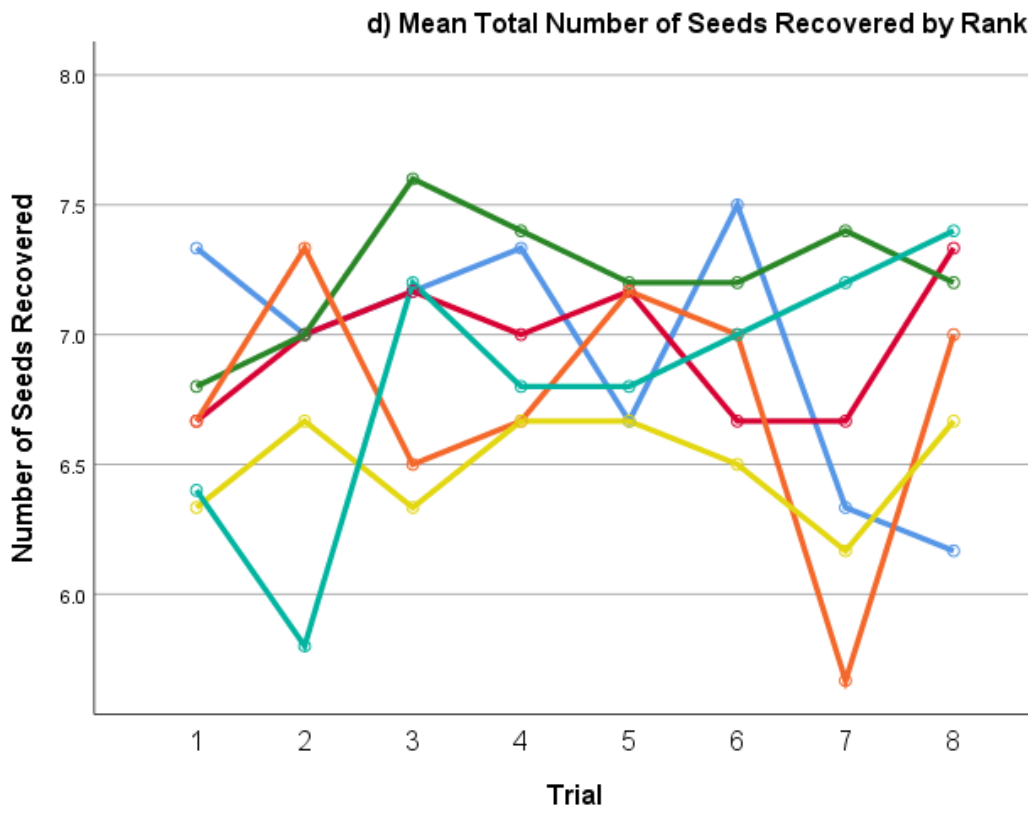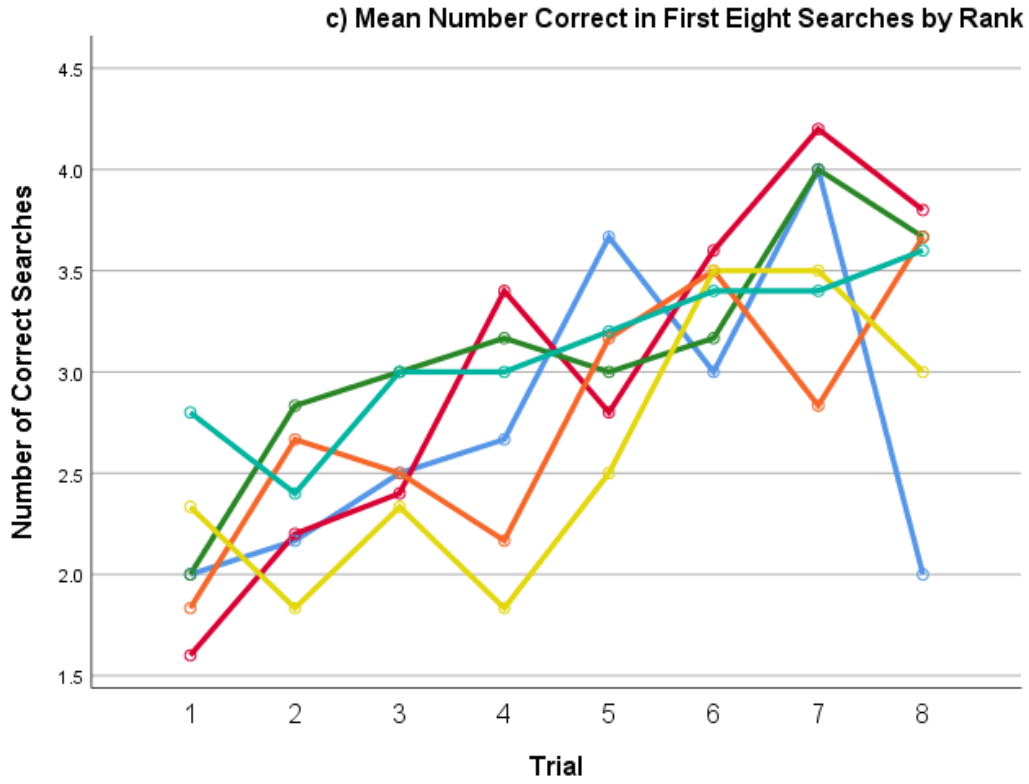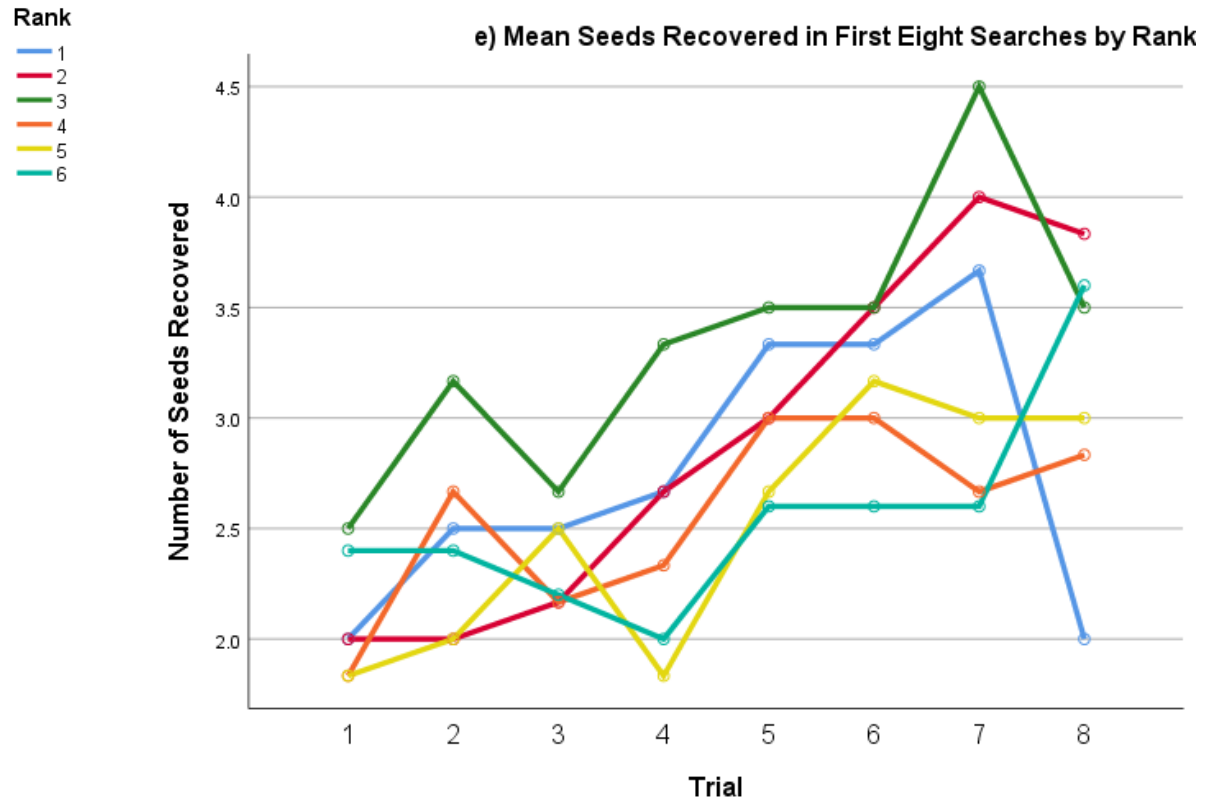
Figure 2.7. Spatial Associative Learning Task. a) Mean Revisits by Rank b) Mean Proportion of Correct Searches by Rank c) Mean Number Correct in First Eight Searches by Rank d) Mean Total Number of Seeds Recovered by Rank e) Mean Seeds Recovered in First Eight Searches by Rank.

$\eta_p^2 = .90$) and post-hoc analyses using Tukey's HSD indicated that flock three performed

significantly better than flocks one ($p = .014$) or six ($p = .012$) (pairwise comparisons in

Appendix F, Table F1).

For the variable 'proportion of correct searches', there was no significant effect of rank

($F(5, 28) = 1.75$, $p = .16$, $\eta_p^2 = .24$), but there was a significant effect of trial ($F(3.65, 102) = 10.3$,

$p < .001$, $\eta_p^2 = .27$; figure 2.7b). In general, the proportion of correct searches increased across

trials (post-hoc Bonferroni pairwise comparisons in Appendix G, Table G1). Mauchly's test

indicated that the assumption of sphericity had been violated ($\chi^2(27) = 65.0$, $p < .001$), so degrees

of freedom were corrected using Greenhouse-Geisser estimates of sphericity ($\varepsilon = 0.52$). There

was no interaction between rank and trial on the proportion of correct searches birds made

($F(18.3, 102) = 0.94$, $p = .54$, $\eta_p^2 = .14$). Sex ($F(1, 27) = 0.72$, $p = .40$, $\eta_p^2 = .026$) and flock ($F(5,$

$28) = 2.06$, $p = .10$, $\eta_p^2 = .27$) did not have significant effects on proportion of correct searches.

For the variable 'number correct in first eight searches', there was no significant effect of

rank ($F(5, 28) = 0.22$, $p = .95$, $\eta_p^2 = .038$), but there was a significant effect of trial ($F(7, 196) =$

6.89, $p < .001$, $\eta_p^2 = .20$; figure 2.7c). In general, the number of correct searches in the first eight

searches increased across trials (post-hoc Bonferroni pairwise comparisons in Appendix H, Table

H1). There was no interaction between rank and trial on the number correct in first eight searches

($F(35, 196) = 0.79$, $p = .80$, $\eta_p^2 = .12$). Sex did not have a significant effect on revisits ($F(1, 27)$

$= 0.18$, $p = .68$, $\eta_p^2 = .007$). Flock had a significant effect on revisits ($F(5, 28) = 7.69$, $p < .001$,

$\eta_p^2 = .58$) and post-hoc analyses using Tukey's HSD indicated that flock three had a significantly

lower number correct in first eight searches than all other flocks (one ($p = .048$), two ($p = .012$),

four ($p < .001$), five ($p < .001$), six ($p = .010$); pairwise comparisons in Appendix H, Table H2).

For the variable, 'total number of seeds recovered', there was no significant effect of rank ($F(5, 28) = 0.22$, $p = .95$, $\eta_p^2 = .038$) or trial ($F(4.27, 120) = 0.95$, $p = .47$, $\eta_p^2 = .033$; figure 2.7d) on total seeds recovered. Mauchly's test indicated that the assumption of sphericity had been violated ($\chi^2(27) = 56.2$, $p = .001$), so degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity ($\varepsilon = 0.61$). There was no interaction between rank and trial on total number of seeds recovered ($F(21.3, 120) = 1.01$, $p = .45$, $\eta_p^2 = .15$). Sex did not have a significant effect on total number of seeds recovered ($F(1, 26) = 1.06$, $p = .31$, $\eta_p^2 = .039$). Flock had a significant effect on total number of seeds recovered ($F(5, 28) = 8.04$, $p < .001$, $\eta_p^2 = .59$) and post-hoc analyses using Tukey's HSD indicated that flock six had significantly less total number of seeds recovered than any other flock (flock one ($p < .001$), flock two ($p = .005$), flock three ($p < .001$), flock four ($p < .001$), and flock five ($p = .013$)) (pairwise comparisons in Appendix I, Table I1).

Finally, 'seeds recovered in first eight searches' had no significant effect of rank ($F(5, 29) = 1.24$, $p = .31$, $\eta_p^2 = .18$), but had a significant effect of trial ($F(4.33, 125) = 5.58$, $p < .001$, $\eta_p^2 = .16$; figure 2.7e). Seeds recovered in the first eight searches generally increased across trials (post-hoc Bonferroni pairwise comparisons in Appendix J, Table J1). Mauchly's test indicated that the assumption of sphericity had been violated ($\chi^2(27) = 50.1$, $p = .004$), so degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity ($\varepsilon = 0.62$). There was no interaction between rank and trial on seeds recovered in first eight searches ($F(21.6, 125) = 0.65$, $p = .88$, $\eta_p^2 = .10$). Sex ($F(1, 27) = 0.44$, $p = .51$, $\eta_p^2 = .016$) did not have a significant effect on total seeds recovered. Flock had a significant effect on total seeds recovered ($F(5, 29) = 3.51$, $p = .013$, $\eta_p^2 = .38$), and post-hoc analyses using Tukey's HSD indicated that flock three

had significantly fewer seeds recovered in first eight searches than flocks four ($p = .031$) or five ($p = .011$) (pairwise comparisons in Appendix J, Table J2).

General Comparisons

Colour and spatial learning task performance. Performance on both the colour associative learning task and the spatial learning task was graphed for each of the variables. The mean number of revisits across all individuals did not show any obvious trends (Figure 2.8). In general, the proportion of correct searches across all individuals increased throughout the trials in both learning tasks. However, birds reached a higher proportion of correct searches on the colour learning task than they did on the spatial learning task (Figure 2.9). The mean number correct in first eight searches also showed a similar pattern. Performance increased across trials in both learning tasks, but birds reached a greater number of correct searches in the colour learning task than they did in the spatial learning task (Figure 2.10). The mean total number of seeds recovered across all individuals showed a different pattern. In the colour task, performance generally increased until the maximum number of seeds were recovered in the last trial. In the spatial task, performance remained relatively constant, and birds only recovered about seven seeds during this set of trials (Figure 2.11). Finally, birds' performance in the mean seeds recovered in first eight searches improved across trials in both spatial and colour learning tasks. However, birds did not recover as many seeds by the end of the spatial task trials as they did by the end of the colour task trials (Figure 2.12). Taken together, birds generally performed better on the colour associative learning task than they did on the spatial associative learning task.

Flock performance. Some exploratory analyses were conducted in order to identify any patterns surrounding flock performance. A tally chart was created showing the number of times a flock performed significantly better or worse than the rest of the flocks (Table 2.3). A greater
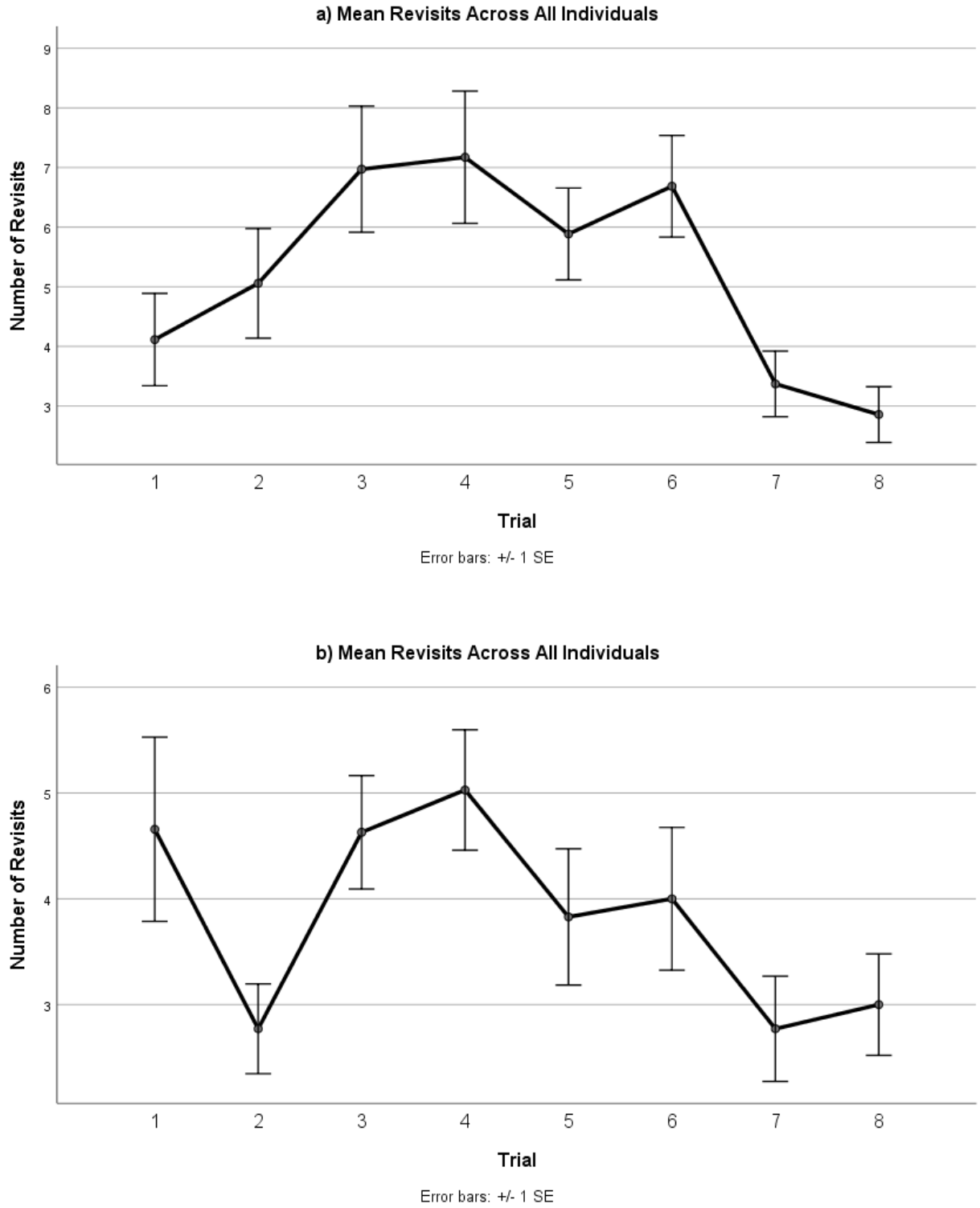
Figure 2.8. Mean Revisits Across All Individuals. a) Colour Associative Learning Task b) Spatial Associative Learning Task.
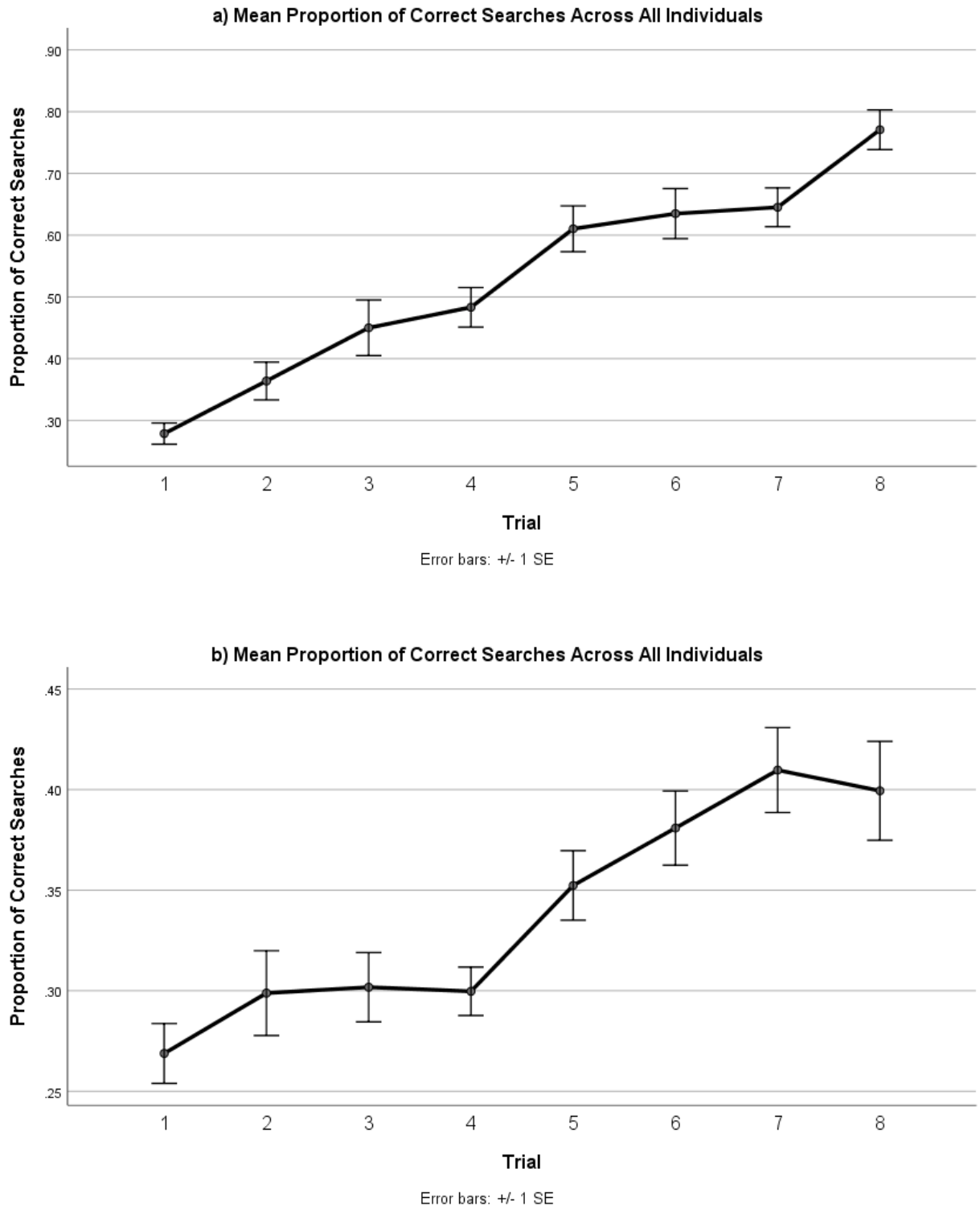
Figure 2.9. Mean Proportion of Correct Searches Across All Individuals. a) Colour Associative

Learning Task b) Spatial Associative Learning Task.
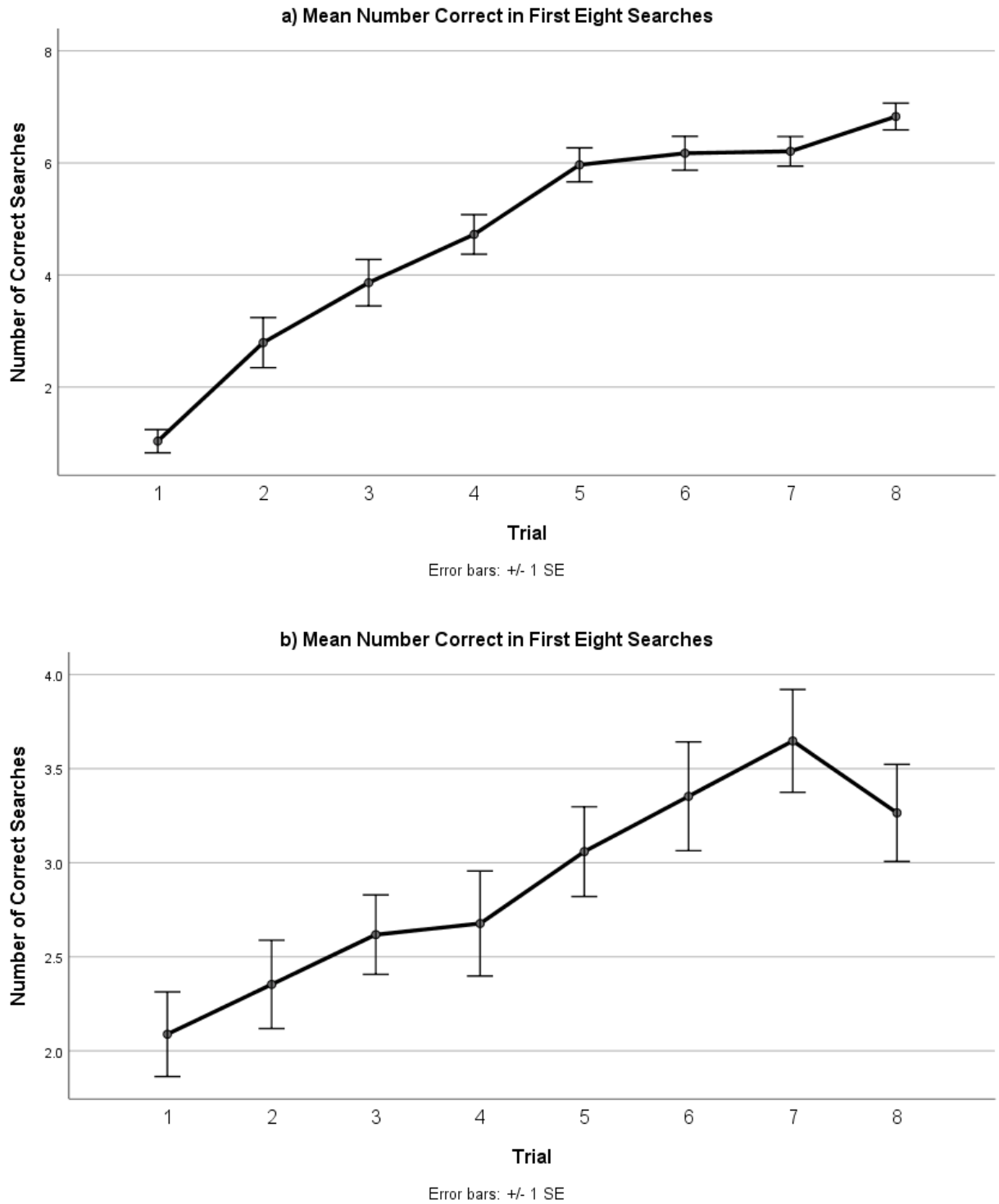
Figure 2.10. Mean Number Correct in First Eight Searches. a) Colour Associative Learning Task

b) Spatial Associative Learning Task.

a) Mean Total Number of Seeds Recovered Across All Individuals

Error bars: +/- 1 SE

b) Mean Total Number of Seeds Recovered Across All Individuals

Error bars: +/- 1 SE
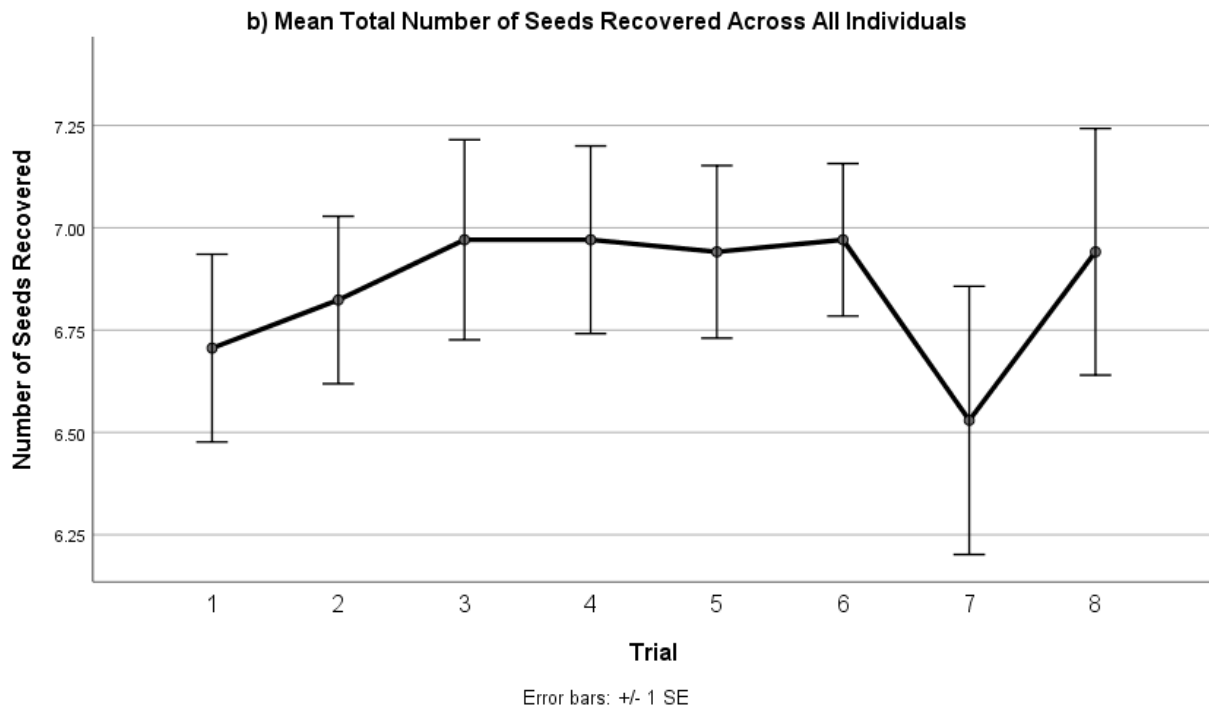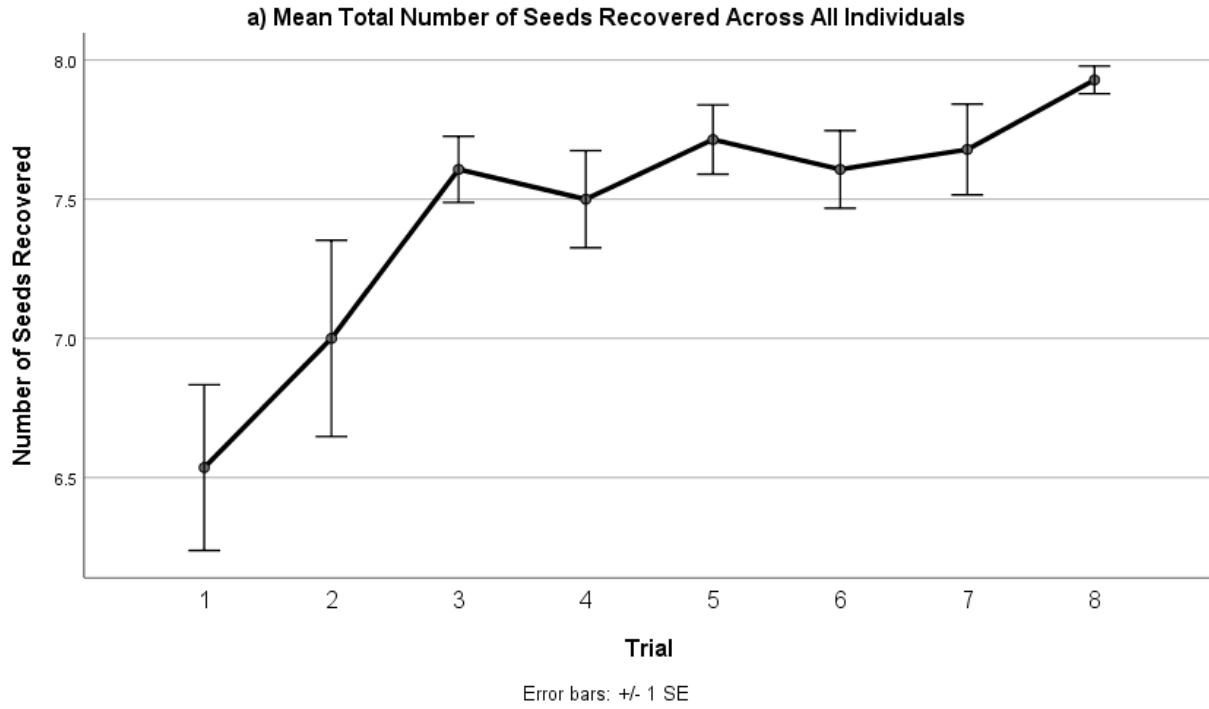
Figure 2.11. Mean Total Number of Seeds Recovered Across All Individuals. a) Colour Associative Learning Task b) Spatial Associative Learning Task.

a) Mean Seeds Recovered in First Eight Searches

Error bars: +/- 1 SE

b) Mean Seeds Recovered in First Eight Searches

Error bars: +/- 1 SE
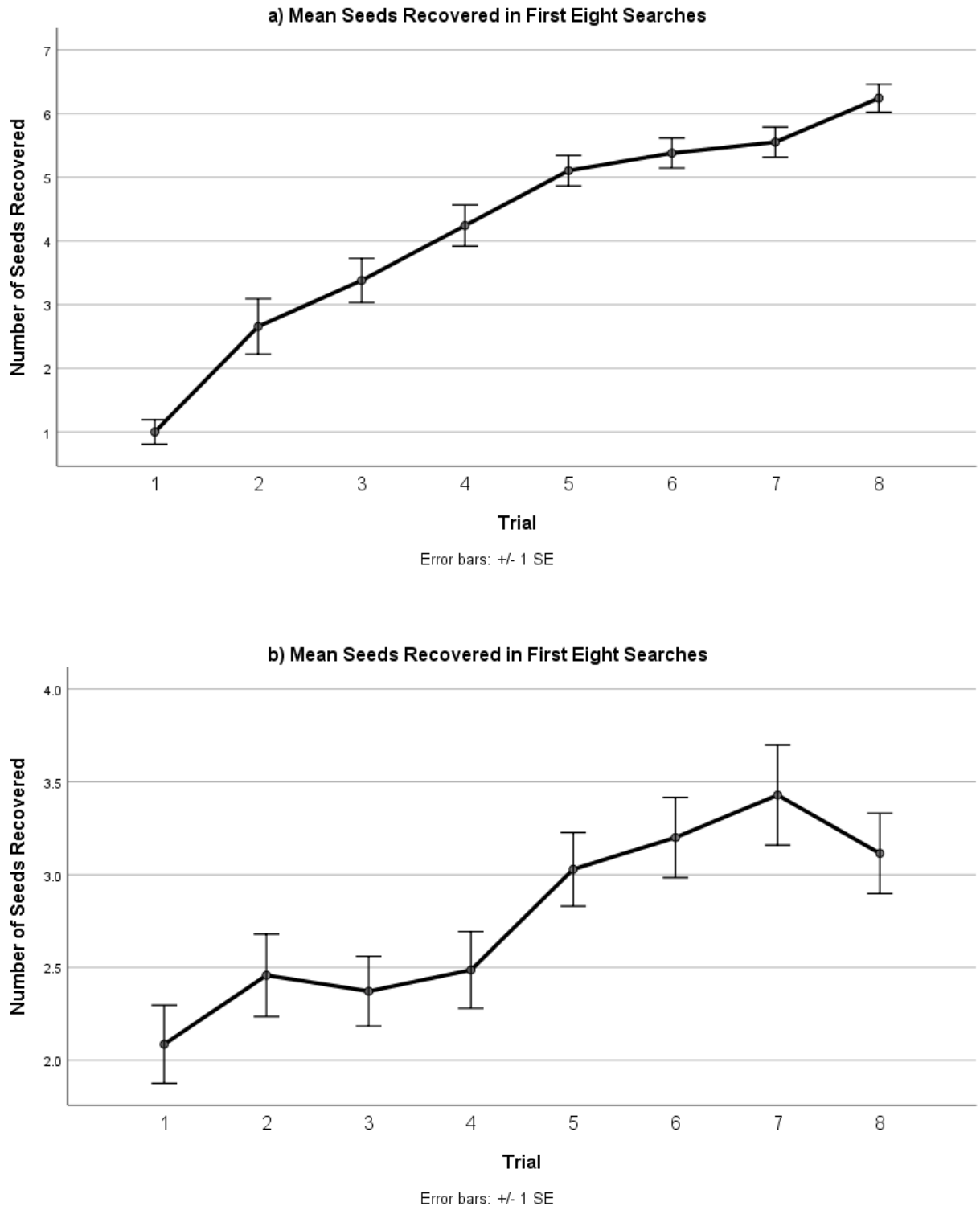
Figure 2.12. Mean Seeds Recovered in First Eight Searches. a) Colour Associative Learning

Task b) Spatial Associative Learning Task.

Table 2.3. Tally Chart of Post-hoc Tukey's HSD Pairwise Comparisons between Flocks. '+' and

'-' symbols indicate performance that was significantly higher or lower in the given flock

relative to another, respectively. Only variables where significant differences were found in Post-

hoc Tukey's HSD pairwise comparisons are shown here. The 'Total' column sums up the

number of times a flock performed significantly higher or lower than another flock.

Flock	Colour Associative Learning Task			Spatial Associative Learning Task				Total
	Proportion of Correct Choices	Number Correct in First Eight Searches	Total Number of Seeds Recovered	Revisits	Number Correct in First Eight Searches	Total Number of Seeds Recovered	Seeds Recovered in First Eight Searches	
1	-	-	-	+	+	+		0
2	-	-	-		+	+		-1
3		-	-	- -	- - - - -	+	- -	-10
4	+ + +				+	+	+	+6
5		+ + +	+ + +		+	+	+	+9
6	-			+	+	-		0

mean was considered better performance in each variable except revisits. In revisits, a lower

mean was considered better performance. Flock means and Post-hoc Tukey's HSD pairwise

comparisons can be found in the appendices. With one exception, flock three performed

consistently worse than the other flocks. Flocks four and five performed consistently better than

the other flocks.

Discussion

Summary of Results

Contrary to the hypothesis, rank had no effect on either the colour or spatial associative

learning tasks for any of the variables measured. Although chickadees were sexed in case of

different behaviour between male and female chickadees on the learning tasks, sex had no effect

on performance. Flocks had variable performance on both the colour and spatial learning tasks,

where flock three almost consistently underperformed while flocks four and five generally

outperformed in comparison to the other flocks (Table 2.3). Although there was some

speculation that flock performance was related to either the time or site of capture, there was no

evidence supporting either idea. Finally, chickadees showed clear evidence of learning on both

the colour and spatial tasks (Figures 2.9 – 2.12).

Working Memory and Reference Memory

Several of the measured variables examined potential differences between working and

reference memory in dominant and subordinate birds. Although no differences were found

among ranks, the variables appeared to be appropriate measures of both types of memory. Since

the colour and spatial tasks were associative learning tasks, they targeted reference memory.

Performance on reference memory measures would be expected to improve as birds learned the

tasks, while performance on working memory measures would be expected to stay relatively

consistent over time because these variables measure birds' memory for their own recent

behaviour.

The 'proportion of correct choices' and the 'number correct in first eight searches' both

measured reference memory. These variables evaluated whether individual birds could choose

learned, baited locations over non-baited ones. A revisit to a previously emptied location was

considered a working memory error as opposed to a reference memory error. As such, revisits to

previously emptied locations were still considered 'correct' reference memory choices. Two

variables were used because some chickadees consistently struggled to find the last few seeds. A

bird could have high accuracy and efficiency recovering the first four or five seeds, while

struggling to recover the remaining few. The 'number correct in first eight searches' was

included to take this into account. Rank did not have a significant effect on reference memory,

but performance across trials significantly increased for the mean 'proportion of correct searches'

(Figure 2.9; Colour Task – Appendix B, Table B1; Spatial Task – Appendix G , Table G1) and

mean 'number correct in first eight searches' (Figure 2.10; Colour Task – Appendix C, Table C1;

Spatial Task – Appendix H, Table H1) in both learning tasks. The learning shown across trials

suggests these variables were good measures of reference memory.

The number of revisits made by birds evaluated working memory, as a bird with 'perfect'

working memory would have made no revisits to previously emptied locations. Therefore, fewer

revisits would have provided evidence for better working memory and consequently, better

cognitive ability of this kind. A chickadee's ability to keep track of the locations it had already

visited should not have changed across trials, as the learning tasks targeted reference memory

learning. Therefore, the number of revisits should have remained consistent. Although the colour

associative learning task showed some significant differences between revisits in different trials, these differences were neither increasing nor decreasing trends (Appendix A, Table A1; Figure 2.8a). The spatial task did not show significant differences in mean revisits across trials (Figure 2.8b). As the number of revisits stayed relatively consistent across trials, this variable appeared to be a good measure of working memory.

Alternative Explanations

Although the results did not support the hypothesis that rank is correlated to cognitive ability in Black-capped Chickadees, there are several alternative explanations to consider. First, it is possible that the learning tasks used were too easy to reveal any underlying differences in learning and memory in Black-capped Chickadees. In the wild, food-storing birds can remember thousands of cache locations, but the learning tasks used here consisted of 48 possible locations (Cowie, Krebs, & Sherry, 1981; Tomback, 1980). However, the chickadees still required time and repeated experience to learn the colour and spatial tasks. For the 'number correct in the first eight searches' variable, birds did not achieve a high level of performance on the colour task until the fifth trial, and reached only moderate levels of performance on the spatial task (Figure 2.10). In addition, the variables measured were sensitive enough to detect differences among flocks in their mean level of performance.

Alternatively, birds may not have been under enough pressure to behave in their respective dominance roles in this captive experiment. When flocks were housed in aviaries, they were housed with two plates of sunflower seeds, and at least three food bowls containing a ground-up mixture of sunflower seeds and bird feed. Since birds were housed in groups of six individuals, there would have been one food bowl available for each bird at almost any given time. Contrastingly, subordinate birds in the wild forage at suboptimal times and locations to

avoid competition with dominant birds (Ficken et al., 1990; Desrochers, 1989). However, ad libitum access to food in the aviaries in this experiment would have prevented subordinate birds from experiencing feeding constraints similar to those experienced in the wild. Furthermore, failure to correctly locate a food cache could mean additional energetic costs and increased predator exposure in the wild. Memory errors in this experiment would have come at no extra cost to subordinates. As a result, it is possible that even if subordinates could make fewer memory errors, they were not adequately motivated to be more selective in their searching behaviour in this captive study.

The Yerkes-Dodson Law adds support to this alternative explanation. This law states that arousal and performance are related to each other in an inverted U-shape with performance increasing until an optimal point of arousal, after which it decreases. Subordinate birds in this experiment may not have reached the stress levels needed for optimal performance on learning tasks. This idea is supported by evidence of stress facilitating learning and memory in rats. Rats reared in chronically stressful environments show increased foraging performance in stressful conditions relative to rats reared in non-stressful environments (Chaby, Sheriff, Hirrlinger, & Braithwaite, 2015). Acute stress also has immediate effects on learning and memory. Rats in a radial arm water maze, solved the maze more quickly at intermediate, mildly stressful temperatures than they did at warmer, low-stress temperatures (Salehi, Cordero, & Sandi, 2010).

There is also evidence of stress facilitating performance in chickadees. Unpredictable food supply was found to increase the efficiency of cache retrieval in Mountain chickadees (*Poecile gambeli*) (Pravosudov & Clayton, 2001). Additionally, long-term elevation of corticosterone, a stress hormone, improved spatial memory and efficiency of cache retrieval in Mountain chickadees (Pravosudov, 2003). In the wild, subordinate chickadees are most

susceptible to chronic and acute stressors absent in this captive experiment. Consequently, subordinates living in high-stress environments with unpredictable food supply could exhibit increased learning and memory performance in comparison to dominant chickadees living in relatively low-stress environments with predictable food supply.

Age, Rank, and Cognitive Ability

There is some recent evidence supporting a relationship between age, dominance, and cognitive ability in chickadees, where older chickadees are more dominant and have better cognitive abilities than younger chickadees. A study by Sonnenberg et al. (2019) studied the relationship between survival and cognitive ability in chickadees. Juvenile chickadees were tested on a spatial learning and reversal task, then followed for survival through the winter. Juveniles who survived to their second winter were the individuals who had initially scored better on the spatial learning and reversal tasks. The performance of this cohort of surviving individuals did not change between the first and second years. However, this cohort made fewer memory errors with the learning and reversal phases of the spatial task compared to a newer cohort of juveniles. This study showed that surviving chickadees have better cognitive abilities than chickadees who did not survive, which would mean that age is positively related to better cognitive abilities. However, this experiment only compared the survivors and non-survivors of one age cohort of chickadees, so it is unclear whether these results can be generalized across different chickadee cohorts.

A study by Tello-Ramos et al. (2018) provides further data. Like the previous study by Sonnenberg et al. (2019), adult chickadees outperformed juveniles in the reversal phase of a spatial task. However, contrary to Sonnenberg et al.'s work, adults did not outperform juveniles in the initial learning phase of the task. Although it is difficult to conclude from these two studies

that adult chickadees have better spatial learning abilities compared to juveniles, in the absence

of trade-offs, natural selection would favor the survival of birds with greater learning abilities. In

fact, female chickadees mated to males with better spatial cognition lay larger broods and fledge

larger clutches compared to females mated to males with comparatively poor spatial cognition

(Branch et al., 2019). These studies provide support for natural selection favouring both the

survival and reproduction of chickadees with greater learning abilities. If chickadees with greater

learning abilities survive longer and are more successful at reproduction, it is likely that age,

dominance, and cognitive ability are all positively related with each other, as age is positively

related to dominance in chickadees (Schubert et al., 2007).

Dominance and Cognitive Ability in Black-capped Chickadees

The only other study in Black-capped Chickadees directly examining the relationship

between dominance and associative learning is the study by Pravosudov et al. (2003) that was

mentioned in chapter one. Like the research presented here, this study also had a spatial

associative learning task and a colour associative learning task. The learning tasks were divided

into two phases. In the first phase, birds were presented with a visible piece of pine nut in one of

70 cache sites. In the second phase, the pine nut was presented in the same location, but the

contents of all cache sites were concealed behind a piece of string. The location of the pine nut

was the cue for the bird in the spatial task of this experiment, whereas a unique colour provided

an additional cue for the pine nut's location in the colour task. Consistent with the results of this

thesis, there was no effect of rank on performance in the colour associative task. However, unlike

the results presented here, dominant chickadees outperformed subordinate chickadees on the

spatial associative learning task. The results of these two studies are mixed, so it is difficult to

conclusively determine whether dominant chickadees have cognitive abilities superior to those of subordinate chickadees.

It is important to consider that individual birds may have different levels of abilities in different areas of cognition. For example, a trade-off seems to exist between spatial learning and cognitive flexibility in chickadees (Tello-Ramos et al., 2019; Croston et al., 2017). Chickadees from higher elevations exhibit increased spatial learning, where they discriminate between rewarding feeders more quickly than chickadees from lower elevations. However, this appears to come at a cost to cognitive flexibility, as chickadees from lower elevations make fewer memory errors than chickadees from higher elevations when the locations of the rewarding feeders are switched. Although there is not enough existing research to accurately describe the relationship between rank and cognitive abilities, some recent findings point towards positive relationships between age, rank and cognitive ability in chickadees. However, the results of this thesis provided no evidence for a positive relationship between rank and cognitive ability, nor any evidence supporting the hypothesis that subordinate chickadees would be better at associative learning than dominant ones.

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CHAPTER THREE

Conclusion

Conclusion

This thesis examined the relationship between rank and associative learning in Black-capped Chickadees. This was done by assessing the dominance rank of chickadees and evaluating their performance on colour and spatial associative learning tasks. The sole previous study examining dominance and cognitive ability in chickadees evaluated dominance through chickadee dyads, but the research here was unique because it evaluated dominance in chickadees in groups representative of natural flocks. The hypothesis of differences in learning and memory between birds of different ranks was not supported.

The research surrounding dominance and cognitive ability has produced mixed results. Contrary to the hypothesis tested here, other recent research in chickadees suggests positive relationships between dominance, cognitive ability, and a third factor – age. More research examining potential trade-offs between different types of cognitive abilities is required. It is possible that dominants and subordinates each excel in different areas of cognition that are related to their respective roles in nature.

Exploring the relationship between social rank and cognitive ability can provide insight into questions surrounding fitness and evolution in animal groups. Having better cognitive abilities could be adaptively advantageous for dominant individuals and help them maintain their dominant status. Alternatively, having better cognitive abilities could explain the persistence of subordinate individuals in animal groups. Although the specifics of this narrative remain unclear, the relationship between social rank and cognitive ability remains a worthwhile area of investigation.

Appendix A

Post-hoc Tests for Revisits in the Colour Associative Learning Task

Table A1

Post-hoc Bonferroni pairwise comparisons between trials for revisits in the colour associative learning task. Significance values at or below p = 0.05 are highlighted for visibility.

(I) trial	(J) trial	Mean Difference (I-J)	Std. Error	Sig.[b]	95% Confidence Interval for Difference[b]	
					Lower Bound	Upper Bound
1	2	-.844	1.162	1.000	-4.843	3.154
	3	-2.950	1.253	.715	-7.260	1.360
	4	-3.044	1.304	.746	-7.528	1.439
	5	-1.661	1.104	1.000	-5.457	2.135
	6	-2.483	1.135	1.000	-6.387	1.420
	7	.750	.798	1.000	-1.996	3.496
	8	1.372	.867	1.000	-1.610	4.354
2	1	.844	1.162	1.000	-3.154	4.843
	3	-2.106	1.172	1.000	-6.136	1.925
	4	-2.200	1.362	1.000	-6.886	2.486
	5	-.817	1.357	1.000	-5.485	3.852
	6	-1.639	1.452	1.000	-6.635	3.357
	7	1.594	1.043	1.000	-1.993	5.182
	8	2.217	1.081	1.000	-1.501	5.934
3	1	2.950	1.253	.715	-1.360	7.260
	2	2.106	1.172	1.000	-1.925	6.136
	4	-.094	1.121	1.000	-3.950	3.762
	5	1.289	1.251	1.000	-3.013	5.591
	6	.467	1.294	1.000	-3.984	4.917
	7	3.700	1.102	.062	-.091	7.491
	8	4.322[*]	1.103	.014	.528	8.116
4	1	3.044	1.304	.746	-1.439	7.528
	2	2.200	1.362	1.000	-2.486	6.886
	3	.094	1.121	1.000	-3.762	3.950
	5	1.383	1.284	1.000	-3.033	5.799
	6	.561	1.544	1.000	-4.750	5.872
	7	3.794	1.301	.189	-.679	8.268
	8	4.417[*]	1.227	.033	.198	8.635

5	1	1.661	1.104	1.000	-2.135	5.457
	2	.817	1.357	1.000	-3.852	5.485
	3	-1.289	1.251	1.000	-5.591	3.013
	4	-1.383	1.284	1.000	-5.799	3.033
	6	-.822	1.134	1.000	-4.721	3.077
	7	2.411	.867	.265	-.572	5.395
	8	3.033	.959	.102	-.264	6.331
6	1	2.483	1.135	1.000	-1.420	6.387
	2	1.639	1.452	1.000	-3.357	6.635
	3	-.467	1.294	1.000	-4.917	3.984
	4	-.561	1.544	1.000	-5.872	4.750
	5	.822	1.134	1.000	-3.077	4.721
	7	3.233	1.124	.208	-.632	7.098
	8	3.856[*]	1.092	.039	.099	7.612
7	1	-.750	.798	1.000	-3.496	1.996
	2	-1.594	1.043	1.000	-5.182	1.993
	3	-3.700	1.102	.062	-7.491	.091
	4	-3.794	1.301	.189	-8.268	.679
	5	-2.411	.867	.265	-5.395	.572
	6	-3.233	1.124	.208	-7.098	.632
	8	.622	.613	1.000	-1.486	2.730
8	1	-1.372	.867	1.000	-4.354	1.610
	2	-2.217	1.081	1.000	-5.934	1.501
	3	-4.322[*]	1.103	.014	-8.116	-.528
	4	-4.417[*]	1.227	.033	-8.635	-.198
	5	-3.033	.959	.102	-6.331	.264
	6	-3.856[*]	1.092	.039	-7.612	-.099
	7	-.622	.613	1.000	-2.730	1.486

Note. Based on estimated marginal means

*. The mean difference is significant at the .05 level.

b. Adjustment for multiple comparisons: Bonferroni.

Table A2

Post-hoc Tukey's HSD pairwise comparisons between flocks for revisits in the colour associative learning task.

(I) Flock	(J) Flock	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	2	1.29	1.118	.854	-2.12	4.70
	3	2.90	1.118	.132	-.51	6.30
	4	3.21	1.118	.074	-.20	6.62
	5	3.10	1.172	.118	-.47	6.68
	6	2.21	1.118	.380	-1.20	5.62
2	1	-1.29	1.118	.854	-4.70	2.12
	3	1.60	1.118	.706	-1.80	5.01
	4	1.92	1.118	.534	-1.49	5.32
	5	1.81	1.172	.639	-1.76	5.39
	6	.92	1.118	.961	-2.49	4.32
3	1	-2.90	1.118	.132	-6.30	.51
	2	-1.60	1.118	.706	-5.01	1.80
	4	.31	1.118	1.000	-3.10	3.72
	5	.21	1.172	1.000	-3.37	3.78
	6	-.69	1.118	.989	-4.10	2.72
4	1	-3.21	1.118	.074	-6.62	.20
	2	-1.92	1.118	.534	-5.32	1.49
	3	-.31	1.118	1.000	-3.72	3.10
	5	-.10	1.172	1.000	-3.68	3.47
	6	-1.00	1.118	.945	-4.41	2.41
5	1	-3.10	1.172	.118	-6.68	.47
	2	-1.81	1.172	.639	-5.39	1.76
	3	-.21	1.172	1.000	-3.78	3.37
	4	.10	1.172	1.000	-3.47	3.68
	6	-.90	1.172	.971	-4.47	2.68
6	1	-2.21	1.118	.380	-5.62	1.20
	2	-.92	1.118	.961	-4.32	2.49
	3	.69	1.118	.989	-2.72	4.10
	4	1.00	1.118	.945	-2.41	4.41
	5	.90	1.172	.971	-2.68	4.47

Based on observed means.

 The error term is Mean Square(Error) = .005.

*. The mean difference is significant at the .05 level.

Appendix B

Post-hoc Tests for Proportion of Correct Searches in the Colour Associative Learning Task

Table B1

Post-hoc Bonferroni pairwise comparisons between trials for proportion of correct searches in the colour associative learning task. Significance values at or below p = 0.05 are highlighted for visibility.

(I) trial	(J) trial	Mean Difference (I-J)	Std. Error	Sig.[b]	95% Confidence Interval for Difference[b] Lower Bound	Upper Bound
1	2	-.083	.034	.650	-.203	.037
	3	-.167	.049	.060	-.337	.004
	4	-.206*	.037	.000	-.335	-.078
	5	-.339*	.043	.000	-.488	-.190
	6	-.356*	.045	.000	-.514	-.198
	7	-.368*	.036	.000	-.493	-.243
	8	-.492*	.036	.000	-.617	-.367
2	1	.083	.034	.650	-.037	.203
	3	-.083	.046	1.000	-.244	.078
	4	-.123	.045	.326	-.281	.035
	5	-.256*	.047	.000	-.421	-.090
	6	-.273*	.054	.001	-.463	-.083
	7	-.285*	.040	.000	-.426	-.144
	8	-.409*	.050	.000	-.583	-.234
3	1	.167	.049	.060	-.004	.337
	2	.083	.046	1.000	-.078	.244
	4	-.040	.055	1.000	-.233	.153
	5	-.172	.054	.103	-.360	.016
	6	-.190	.071	.375	-.438	.059
	7	-.202*	.054	.025	-.389	-.015
	8	-.325*	.056	.000	-.521	-.129
4	1	.206*	.037	.000	.078	.335
	2	.123	.045	.326	-.035	.281
	3	.040	.055	1.000	-.153	.233
	5	-.133	.041	.097	-.276	.011
	6	-.150	.054	.278	-.338	.038

	7	-.162*	.043	.023	-.311	-.013
	8	-.286*	.047	.000	-.450	-.121
5	1	.339*	.043	.000	.190	.488
	2	.256*	.047	.000	.090	.421
	3	.172	.054	.103	-.016	.360
	4	.133	.041	.097	-.011	.276
	6	-.017	.047	1.000	-.181	.146
	7	-.029	.040	1.000	-.170	.111
	8	-.153	.052	.188	-.334	.028
6	1	.356*	.045	.000	.198	.514
	2	.273*	.054	.001	.083	.463
	3	.190	.071	.375	-.059	.438
	4	.150	.054	.278	-.038	.338
	5	.017	.047	1.000	-.146	.181
	7	-.012	.046	1.000	-.173	.149
	8	-.136	.047	.219	-.300	.028
7	1	.368*	.036	.000	.243	.493
	2	.285*	.040	.000	.144	.426
	3	.202*	.054	.025	.015	.389
	4	.162*	.043	.023	.013	.311
	5	.029	.040	1.000	-.111	.170
	6	.012	.046	1.000	-.149	.173
	8	-.124	.041	.153	-.266	.019
8	1	.492*	.036	.000	.367	.617
	2	.409*	.050	.000	.234	.583
	3	.325*	.056	.000	.129	.521
	4	.286*	.047	.000	.121	.450
	5	.153	.052	.188	-.028	.334
	6	.136	.047	.219	-.028	.300
	7	.124	.041	.153	-.019	.266

Based on estimated marginal means

*. The mean difference is significant at the .05 level.

b. Adjustment for multiple comparisons: Bonferroni.

Table B2

Post-hoc Tukey's HSD pairwise comparisons between flocks for proportion of correct searches in the colour associative learning task. Significance values at or below p = 0.05 are highlighted for visibility.

(I) Flock	(J) Flock	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	2	-.0117	.04132	1.000	-.1390	.1157
	3	-.0448	.04132	.883	-.1721	.0825
	4	-.1412*	.04132	.023	-.2686	-.0139
	5	-.1110	.04620	.193	-.2534	.0313
	6	.0202	.05061	.999	-.1358	.1762
2	1	.0117	.04132	1.000	-.1157	.1390
	3	-.0331	.04132	.965	-.1605	.0942
	4	-.1296*	.04132	.044	-.2569	-.0022
	5	-.0994	.04620	.295	-.2417	.0430
	6	.0319	.05061	.988	-.1241	.1878
3	1	.0448	.04132	.883	-.0825	.1721
	2	.0331	.04132	.965	-.0942	.1605
	4	-.0965	.04132	.218	-.2238	.0309
	5	-.0663	.04620	.707	-.2086	.0761
	6	.0650	.05061	.790	-.0910	.2210
4	1	.1412*	.04132	.023	.0139	.2686
	2	.1296*	.04132	.044	.0022	.2569
	3	.0965	.04132	.218	-.0309	.2238
	5	.0302	.04620	.985	-.1122	.1726
	6	.1615*	.05061	.039	.0055	.3174
5	1	.1110	.04620	.193	-.0313	.2534
	2	.0994	.04620	.295	-.0430	.2417
	3	.0663	.04620	.707	-.0761	.2086
	4	-.0302	.04620	.985	-.1726	.1122
	6	.1312	.05466	.194	-.0372	.2997
6	1	-.0202	.05061	.999	-.1762	.1358
	2	-.0319	.05061	.988	-.1878	.1241
	3	-.0650	.05061	.790	-.2210	.0910
	4	-.1615*	.05061	.039	-.3174	-.0055
	5	-.1312	.05466	.194	-.2997	.0372

Based on observed means.

 The error term is Mean Square(Error) = .005.

*. The mean difference is significant at the .05 level.

Appendix C

Post-hoc Tests for Number Correct in First Eight Searches in the Colour Associative Learning
Task

Table C1

*Post-hoc Bonferroni pairwise comparisons between trials for number correct in first eight
searches in the colour associative learning task. Significance values at or below p = 0.05 are
highlighted for visibility.*

(I) trial	(J) trial	Mean Difference (I-J)	Std. Error	Sig.[b]	95% Confidence Interval for Difference[b]	
					Lower Bound	Upper Bound
1	2	-1.767	.548	.105	-3.701	.168
	3	-2.900*	.413	.000	-4.360	-1.440
	4	-3.742*	.401	.000	-5.159	-2.324
	5	-4.917*	.329	.000	-6.079	-3.754
	6	-5.150*	.422	.000	-6.642	-3.658
	7	-5.208*	.369	.000	-6.510	-3.907
	8	-5.800*	.354	.000	-7.052	-4.548
2	1	1.767	.548	.105	-.168	3.701
	3	-1.133	.592	1.000	-3.223	.957
	4	-1.975*	.535	.034	-3.864	-.086
	5	-3.150*	.598	.001	-5.261	-1.039
	6	-3.383*	.505	.000	-5.165	-1.602
	7	-3.442*	.549	.000	-5.382	-1.501
	8	-4.033*	.438	.000	-5.578	-2.488
3	1	2.900*	.413	.000	1.440	4.360
	2	1.133	.592	1.000	-.957	3.223
	4	-.842	.515	1.000	-2.660	.976
	5	-2.017*	.518	.020	-3.844	-.189
	6	-2.250*	.492	.004	-3.989	-.511
	7	-2.308*	.433	.001	-3.838	-.778
	8	-2.900*	.431	.000	-4.421	-1.379
4	1	3.742*	.401	.000	2.324	5.159
	2	1.975*	.535	.034	.086	3.864
	3	.842	.515	1.000	-.976	2.660
	5	-1.175	.441	.387	-2.732	.382

	6	-1.408*	.373	.028	-2.727	-.090
	7	-1.467*	.375	.020	-2.791	-.142
	8	-2.058*	.478	.007	-3.745	-.371
5	1	4.917*	.329	.000	3.754	6.079
	2	3.150*	.598	.001	1.039	5.261
	3	2.017*	.518	.020	.189	3.844
	4	1.175	.441	.387	-.382	2.732
	6	-.233	.401	1.000	-1.649	1.182
	7	-.292	.404	1.000	-1.717	1.134
	8	-.883	.388	.910	-2.254	.487
6	1	5.150*	.422	.000	3.658	6.642
	2	3.383*	.505	.000	1.602	5.165
	3	2.250*	.492	.004	.511	3.989
	4	1.408*	.373	.028	.090	2.727
	5	.233	.401	1.000	-1.182	1.649
	7	-.058	.300	1.000	-1.117	1.001
	8	-.650	.383	1.000	-2.004	.704
7	1	5.208*	.369	.000	3.907	6.510
	2	3.442*	.549	.000	1.501	5.382
	3	2.308*	.433	.001	.778	3.838
	4	1.467*	.375	.020	.142	2.791
	5	.292	.404	1.000	-1.134	1.717
	6	.058	.300	1.000	-1.001	1.117
	8	-.592	.381	1.000	-1.939	.755
8	1	5.800*	.354	.000	4.548	7.052
	2	4.033*	.438	.000	2.488	5.578
	3	2.900*	.431	.000	1.379	4.421
	4	2.058*	.478	.007	.371	3.745
	5	.883	.388	.910	-.487	2.254
	6	.650	.383	1.000	-.704	2.004
	7	.592	.381	1.000	-.755	1.939

Based on estimated marginal means

*. The mean difference is significant at the .05 level.

b. Adjustment for multiple comparisons: Bonferroni.

Table C2

Post-hoc Tukey's HSD pairwise comparisons between flocks for number correct in first eight searches in the colour associative learning task. Significance values at or below p = 0.05 are highlighted for visibility.

(I) Flock	(J) Flock	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	2	-.06	.319	1.000	-1.00	.88
	3	-.25	.319	.933	-1.19	.69
	4	-.85	.319	.087	-1.79	.08
	5	-1.32*	.334	.005	-2.31	-.34
2	1	.06	.319	1.000	-.88	1.00
	3	-.19	.319	.975	-1.13	.75
	4	-.79	.319	.128	-1.73	.15
	5	-1.26*	.334	.008	-2.24	-.27
3	1	.25	.319	.933	-.69	1.19
	2	.19	.319	.975	-.75	1.13
	4	-.60	.319	.346	-1.54	.33
	5	-1.07*	.334	.028	-2.06	-.09
4	1	.85	.319	.087	-.08	1.79
	2	.79	.319	.128	-.15	1.73
	3	.60	.319	.346	-.33	1.54
	5	-.47	.334	.635	-1.45	.52
5	1	1.32*	.334	.005	.34	2.31
	2	1.26*	.334	.008	.27	2.24
	3	1.07*	.334	.028	.09	2.06
	4	.47	.334	.635	-.52	1.45

Based on estimated marginal means

*. The mean difference is significant at the .05 level.

b. Adjustment for multiple comparisons: Bonferroni.

Appendix D

Post-hoc Tests for Total Number of Seeds Recovered in the Colour Associative Learning Task

Table D1

Post-hoc Bonferroni pairwise comparisons between trials for total number of seeds recovered in the colour associative learning task. Significance values at or below p = 0.05 are highlighted for visibility.

(I) trial	(J) trial	Mean Difference (I-J)	Std. Error	Sig.b	95% Confidence Interval for Difference[b] Lower Bound	Upper Bound
1	2	-.492	.489	1.000	-2.229	1.246
	3	-1.092	.318	.067	-2.223	.039
	4	-.992	.281	.053	-1.990	.007
	5	-1.225*	.317	.023	-2.350	-.100
	6	-1.117	.327	.069	-2.277	.044
	7	-1.192*	.335	.049	-2.381	-.002
	8	-1.433*	.311	.004	-2.537	-.330
2	1	.492	.489	1.000	-1.246	2.229
	3	-.600	.383	1.000	-1.961	.761
	4	-.500	.403	1.000	-1.930	.930
	5	-.733	.329	1.000	-1.902	.435
	6	-.625	.313	1.000	-1.736	.486
	7	-.700	.283	.601	-1.704	.304
	8	-.942	.339	.309	-2.147	.264
3	1	1.092	.318	.067	-.039	2.223
	2	.600	.383	1.000	-.761	1.961
	4	.100	.170	1.000	-.504	.704
	5	-.133	.136	1.000	-.615	.348
	6	-.025	.150	1.000	-.559	.509
	7	-.100	.187	1.000	-.763	.563
	8	-.342	.118	.241	-.762	.079
4	1	.992	.281	.053	-.007	1.990
	2	.500	.403	1.000	-.930	1.930
	3	-.100	.170	1.000	-.704	.504
	5	-.233	.143	1.000	-.740	.273
	6	-.125	.165	1.000	-.710	.460

	7	-.200	.187	1.000	-.863	.463
	8	-.442	.155	.256	-.991	.107
5	1	1.225*	.317	.023	.100	2.350
	2	.733	.329	1.000	-.435	1.902
	3	.133	.136	1.000	-.348	.615
	4	.233	.143	1.000	-.273	.740
	6	.108	.095	1.000	-.231	.447
	7	.033	.092	1.000	-.295	.362
	8	-.208	.095	1.000	-.547	.131
6	1	1.117	.327	.069	-.044	2.277
	2	.625	.313	1.000	-.486	1.736
	3	.025	.150	1.000	-.509	.559
	4	.125	.165	1.000	-.460	.710
	5	-.108	.095	1.000	-.447	.231
	7	-.075	.084	1.000	-.375	.225
	8	-.317	.110	.247	-.708	.075
7	1	1.192*	.335	.049	.002	2.381
	2	.700	.283	.601	-.304	1.704
	3	.100	.187	1.000	-.563	.763
	4	.200	.187	1.000	-.463	.863
	5	-.033	.092	1.000	-.362	.295
	6	.075	.084	1.000	-.225	.375
	8	-.242	.128	1.000	-.696	.212
8	1	1.433*	.311	.004	.330	2.537
	2	.942	.339	.309	-.264	2.147
	3	.342	.118	.241	-.079	.762
	4	.442	.155	.256	-.107	.991
	5	.208	.095	1.000	-.131	.547
	6	.317	.110	.247	-.075	.708
	7	.242	.128	1.000	-.212	.696

Based on estimated marginal means

*. The mean difference is significant at the .05 level.

b. Adjustment for multiple comparisons: Bonferroni.

Appendix E

Post-hoc Tests for Seeds Recovered in First Eight Searches in the Colour Associative Learning Task

Table E1

Post-hoc Bonferroni pairwise comparisons between trials for total number of seeds recovered in the colour associative learning task. Significance values at or below p = 0.05 are highlighted for visibility.

(I) Trial	(J) Trial	Mean Difference (I-J)	Std. Error	Sig.[b]	95% Confidence Interval for Difference[b] Lower Bound	Upper Bound
1	2	-1.667	.542	.151	-3.582	.248
	3	-2.425[*]	.380	.000	-3.766	-1.084
	4	-3.300[*]	.345	.000	-4.518	-2.082
	5	-4.100[*]	.312	.000	-5.201	-2.999
	6	-4.400[*]	.330	.000	-5.564	-3.236
	7	-4.567[*]	.332	.000	-5.737	-3.396
	8	-5.258[*]	.344	.000	-6.473	-4.044
2	1	1.667	.542	.151	-.248	3.582
	3	-.758	.576	1.000	-2.793	1.277
	4	-1.633	.528	.143	-3.497	.230
	5	-2.433[*]	.549	.005	-4.372	-.495
	6	-2.733[*]	.497	.000	-4.488	-.978
	7	-2.900[*]	.533	.000	-4.783	-1.017
	8	-3.592[*]	.457	.000	-5.206	-1.978
3	1	2.425[*]	.380	.000	1.084	3.766
	2	.758	.576	1.000	-1.277	2.793
	4	-.875	.433	1.000	-2.403	.653
	5	-1.675[*]	.405	.011	-3.106	-.244
	6	-1.975[*]	.378	.001	-3.311	-.639
	7	-2.142[*]	.389	.000	-3.516	-.767
	8	-2.833[*]	.378	.000	-4.169	-1.497
4	1	3.300[*]	.345	.000	2.082	4.518
	2	1.633	.528	.143	-.230	3.497
	3	.875	.433	1.000	-.653	2.403
	5	-.800	.432	1.000	-2.325	.725

	6	-1.100	.356	.145	-2.358	.158
	7	-1.267*	.354	.045	-2.518	-.015
	8	-1.958*	.469	.010	-3.614	-.303
5	1	4.100*	.312	.000	2.999	5.201
	2	2.433*	.549	.005	.495	4.372
	3	1.675*	.405	.011	.244	3.106
	4	.800	.432	1.000	-.725	2.325
	6	-.300	.295	1.000	-1.341	.741
	7	-.467	.322	1.000	-1.605	.671
	8	-1.158*	.299	.021	-2.214	-.103
6	1	4.400*	.330	.000	3.236	5.564
	2	2.733*	.497	.000	.978	4.488
	3	1.975*	.378	.001	.639	3.311
	4	1.100	.356	.145	-.158	2.358
	5	.300	.295	1.000	-.741	1.341
	7	-.167	.289	1.000	-1.186	.853
	8	-.858	.349	.614	-2.091	.375
7	1	4.567*	.332	.000	3.396	5.737
	2	2.900*	.533	.000	1.017	4.783
	3	2.142*	.389	.000	.767	3.516
	4	1.267*	.354	.045	.015	2.518
	5	.467	.322	1.000	-.671	1.605
	6	.167	.289	1.000	-.853	1.186
	8	-.692	.363	1.000	-1.973	.589
8	1	5.258*	.344	.000	4.044	6.473
	2	3.592*	.457	.000	1.978	5.206
	3	2.833*	.378	.000	1.497	4.169
	4	1.958*	.469	.010	.303	3.614
	5	1.158*	.299	.021	.103	2.214
	6	.858	.349	.614	-.375	2.091
	7	.692	.363	1.000	-.589	1.973

Based on estimated marginal means

*. The mean difference is significant at the .05 level.

b. Adjustment for multiple comparisons: Bonferroni.

Table E2

Post-hoc Tukey's HSD pairwise comparisons between flocks for total number of seeds recovered in the colour associative learning task. Significance values at or below p = 0.05 are highlighted for visibility.

(I) Flock	(J) Flock	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval Lower Bound	Upper Bound
1	2	-.04	.253	1.000	-.79	.70
	3	-.29	.253	.778	-1.04	.45
	4	-.60	.253	.153	-1.35	.14
	5	-1.09*	.266	.003	-1.87	-.31
2	1	.04	.253	1.000	-.70	.79
	3	-.25	.253	.858	-1.00	.50
	4	-.56	.253	.206	-1.31	.18
	5	-1.05*	.266	.005	-1.83	-.26
3	1	.29	.253	.778	-.45	1.04
	2	.25	.253	.858	-.50	1.00
	4	-.31	.253	.732	-1.06	.43
	5	-.80*	.266	.045	-1.58	-.01
4	1	.60	.253	.153	-.14	1.35
	2	.56	.253	.206	-.18	1.31
	3	.31	.253	.732	-.43	1.06
	5	-.48	.266	.386	-1.27	.30
5	1	1.09*	.266	.003	.31	1.87
	2	1.05*	.266	.005	.26	1.83
	3	.80*	.266	.045	.01	1.58
	4	.48	.266	.386	-.30	1.27

Based on observed means.

 The error term is Mean Square(Error) = .192.

*. The mean difference is significant at the .05 level.

Appendix F

Post-hoc Tests for Revisits in the Spatial Associative Learning Task

Table F1

Post-hoc Tukey's HSD pairwise comparisons between flocks for revisits in the spatial associative learning task. Significance values at or below p = 0.05 are highlighted for visibility.

(I) Flock	(J) Flock	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	2	-.65	.815	.967	-3.13	1.84
	3	-2.92*	.815	.014	-5.40	-.43
	4	-1.29	.815	.615	-3.78	1.19
	5	-1.41	.855	.572	-4.02	1.19
	6	.06	.815	1.000	-2.42	2.55
2	1	.65	.815	.967	-1.84	3.13
	3	-2.27	.815	.089	-4.76	.21
	4	-.65	.815	.967	-3.13	1.84
	5	-.77	.855	.944	-3.37	1.84
	6	.71	.815	.951	-1.78	3.19
3	1	2.92*	.815	.014	.43	5.40
	2	2.27	.815	.089	-.21	4.76
	4	1.63	.815	.370	-.86	4.11
	5	1.50	.855	.506	-1.10	4.11
	6	2.98*	.815	.012	.49	5.46
4	1	1.29	.815	.615	-1.19	3.78
	2	.65	.815	.967	-1.84	3.13
	3	-1.62	.815	.370	-4.11	.86
	5	-.12	.855	1.000	-2.73	2.49
	6	1.35	.815	.567	-1.13	3.84
5	1	1.41	.855	.572	-1.19	4.02
	2	.77	.855	.944	-1.84	3.37
	3	-1.50	.855	.506	-4.11	1.10
	4	.12	.855	1.000	-2.49	2.73
	6	1.47	.855	.527	-1.13	4.08
6	1	-.06	.815	1.000	-2.55	2.42
	2	-.71	.815	.951	-3.19	1.78
	3	-2.98*	.815	.012	-5.46	-.49

4	-1.35	.815	.567	-3.84	1.13
5	-1.47	.855	.527	-4.08	1.13

Based on observed means.

 The error term is Mean Square(Error) = 1.993.

*. The mean difference is significant at the .05 level.

Appendix G

Post-hoc Tests for Proportion of Correct Searches in the Spatial Associative Learning Task

Table G1

Post-hoc Bonferroni pairwise comparisons between trials for proportion of correct searches in the spatial associative learning task. Significance values at or below p = 0.05 are highlighted for visibility.

(I) trial	(J) trial	Mean Difference (I-J)	Std. Error	Sig.[b]	95% Confidence Interval for Difference[b]	
					Lower Bound	Upper Bound
1	2	-.028	.016	1.000	-.084	.027
	3	-.031	.020	1.000	-.099	.037
	4	-.030	.019	1.000	-.095	.034
	5	-.082	.026	.117	-.173	.009
	6	-.111[*]	.023	.001	-.191	-.031
	7	-.139[*]	.027	.001	-.234	-.045
	8	-.134[*]	.027	.001	-.226	-.041
2	1	.028	.016	1.000	-.027	.084
	3	-.002	.026	1.000	-.091	.086
	4	-.002	.025	1.000	-.087	.084
	5	-.054	.033	1.000	-.169	.062
	6	-.083	.029	.203	-.181	.016
	7	-.111	.033	.071	-.226	.005
	8	-.105	.031	.059	-.212	.002
3	1	.031	.020	1.000	-.037	.099
	2	.002	.026	1.000	-.086	.091
	4	.000	.017	1.000	-.058	.058
	5	-.051	.021	.620	-.125	.022
	6	-.080[*]	.022	.030	-.156	-.004
	7	-.108[*]	.024	.003	-.192	-.025
	8	-.103[*]	.028	.025	-.199	-.007
4	1	.030	.019	1.000	-.034	.095
	2	.002	.025	1.000	-.084	.087
	3	.000	.017	1.000	-.058	.058
	5	-.052	.022	.696	-.127	.024
	6	-.081[*]	.019	.004	-.145	-.017

	7	-.109*	.022	.001	-.185	-.033
	8	-.103*	.022	.001	-.178	-.029
5	1	.082	.026	.117	-.009	.173
	2	.054	.033	1.000	-.062	.169
	3	.051	.021	.620	-.022	.125
	4	.052	.022	.696	-.024	.127
	6	-.029	.019	1.000	-.093	.035
	7	-.057*	.016	.030	-.111	-.003
	8	-.051	.024	1.000	-.135	.032
6	1	.111*	.023	.001	.031	.191
	2	.083	.029	.203	-.016	.181
	3	.080*	.022	.030	.004	.156
	4	.081*	.019	.004	.017	.145
	5	.029	.019	1.000	-.035	.093
	7	-.028	.016	1.000	-.084	.028
	8	-.023	.023	1.000	-.103	.058
7	1	.139*	.027	.001	.045	.234
	2	.111	.033	.071	-.005	.226
	3	.108*	.024	.003	.025	.192
	4	.109*	.022	.001	.033	.185
	5	.057*	.016	.030	.003	.111
	6	.028	.016	1.000	-.028	.084
	8	.005	.022	1.000	-.070	.081
8	1	.134*	.027	.001	.041	.226
	2	.105	.031	.059	-.002	.212
	3	.103*	.028	.025	.007	.199
	4	.103*	.022	.001	.029	.178
	5	.051	.024	1.000	-.032	.135
	6	.023	.023	1.000	-.058	.103
	7	-.005	.022	1.000	-.081	.070

Based on estimated marginal means

*. The mean difference is significant at the .05 level.

b. Adjustment for multiple comparisons: Bonferroni.

Appendix H

Post-hoc Tests for Number Correct in First Eight Searches in the Spatial Associative Learning
Task

Table H1

*Post-hoc Bonferroni pairwise comparisons between trials for number correct first eight searches
in the spatial associative learning task. Significance values at or below p = 0.05 are highlighted
for visibility.*

(I) trial	(J) trial	Mean Difference (I-J)	Std. Error	Sig.[b]	95% Confidence Interval for Difference[b]	
					Lower Bound	Upper Bound
1	2	-.256	.173	1.000	-.854	.343
	3	-.528	.257	1.000	-1.415	.360
	4	-.611	.292	1.000	-1.619	.397
	5	-.961	.318	.148	-2.058	.136
	6	-1.267*	.316	.011	-2.357	-.177
	7	-1.561*	.311	.001	-2.634	-.489
	8	-1.194*	.286	.007	-2.180	-.208
2	1	.256	.173	1.000	-.343	.854
	3	-.272	.240	1.000	-1.101	.557
	4	-.356	.288	1.000	-1.349	.638
	5	-.706	.334	1.000	-1.857	.446
	6	-1.011*	.286	.041	-2.000	-.022
	7	-1.306*	.312	.007	-2.382	-.229
	8	-.939	.295	.101	-1.959	.081
3	1	.528	.257	1.000	-.360	1.415
	2	.272	.240	1.000	-.557	1.101
	4	-.083	.236	1.000	-.897	.730
	5	-.433	.333	1.000	-1.584	.717
	6	-.739	.289	.460	-1.738	.260
	7	-1.033	.321	.092	-2.143	.076
	8	-.667	.290	.815	-1.667	.334
4	1	.611	.292	1.000	-.397	1.619
	2	.356	.288	1.000	-.638	1.349
	3	.083	.236	1.000	-.730	.897

	5	-.350	.316	1.000	-1.440	.740
	6	-.656	.295	.960	-1.672	.361
	7	-.950	.336	.241	-2.111	.211
	8	-.583	.325	1.000	-1.704	.537
5	1	.961	.318	.148	-.136	2.058
	2	.706	.334	1.000	-.446	1.857
	3	.433	.333	1.000	-.717	1.584
	4	.350	.316	1.000	-.740	1.440
	6	-.306	.270	1.000	-1.239	.628
	7	-.600	.281	1.000	-1.570	.370
	8	-.233	.266	1.000	-1.152	.685
6	1	1.267*	.316	.011	.177	2.357
	2	1.011*	.286	.041	.022	2.000
	3	.739	.289	.460	-.260	1.738
	4	.656	.295	.960	-.361	1.672
	5	.306	.270	1.000	-.628	1.239
	7	-.294	.242	1.000	-1.130	.541
	8	.072	.297	1.000	-.953	1.098
7	1	1.561*	.311	.001	.489	2.634
	2	1.306*	.312	.007	.229	2.382
	3	1.033	.321	.092	-.076	2.143
	4	.950	.336	.241	-.211	2.111
	5	.600	.281	1.000	-.370	1.570
	6	.294	.242	1.000	-.541	1.130
	8	.367	.247	1.000	-.486	1.219
8	1	1.194*	.286	.007	.208	2.180
	2	.939	.295	.101	-.081	1.959
	3	.667	.290	.815	-.334	1.667
	4	.583	.325	1.000	-.537	1.704
	5	.233	.266	1.000	-.685	1.152
	6	-.072	.297	1.000	-1.098	.953
	7	-.367	.247	1.000	-1.219	.486

Based on estimated marginal means

*. The mean difference is significant at the .05 level.

b. Adjustment for multiple comparisons: Bonferroni.

Table H2

Post-hoc Tukey's HSD pairwise comparisons between flocks for number correct in first eight searches in the spatial associative learning task. Significance values at or below p = 0.05 are highlighted for visibility.

(I) Flock	(J) Flock	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
1	2	-.23	.400	.992	-1.45	.99
	3	1.23*	.400	.048	.01	2.45
	4	-.98	.400	.174	-2.20	.24
	5	-.87	.419	.333	-2.15	.41
	6	-.34	.419	.962	-1.62	.94
2	1	.23	.400	.992	-.99	1.45
	3	1.46*	.400	.012	.24	2.68
	4	-.75	.400	.437	-1.97	.47
	5	-.64	.419	.655	-1.92	.64
	6	-.11	.419	1.000	-1.39	1.17
3	1	-1.23*	.400	.048	-2.45	-.01
	2	-1.46*	.400	.012	-2.68	-.24
	4	-2.21*	.400	.000	-3.43	-.99
	5	-2.10*	.419	.000	-3.38	-.81
	6	-1.57*	.419	.010	-2.85	-.29
4	1	.98	.400	.174	-.24	2.20
	2	.75	.400	.437	-.47	1.97
	3	2.21*	.400	.000	.99	3.43
	5	.11	.419	1.000	-1.17	1.39
	6	.64	.419	.655	-.64	1.92
5	1	.87	.419	.333	-.41	2.15
	2	.64	.419	.655	-.64	1.92
	3	2.10*	.419	.000	.81	3.38
	4	-.11	.419	1.000	-1.39	1.17
	6	.53	.438	.834	-.81	1.86
6	1	.34	.419	.962	-.94	1.62
	2	.11	.419	1.000	-1.17	1.39
	3	1.57*	.419	.010	.29	2.85
	4	-.64	.419	.655	-1.92	.64
	5	-.53	.438	.834	-1.86	.81

Based on observed means.

 The error term is Mean Square(Error) = .480.

*. The mean difference is significant at the .05 level.

Appendix I

Post-hoc Tests for Total Number of Seeds Recovered in the Spatial Associative Learning Task

Table I1

Post-hoc Tukey's HSD pairwise comparisons between flocks for total number of seeds recovered in the spatial associative learning task. Significance values at or below p = 0.05 are highlighted for visibility.

(I) Flock	(J) Flock	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval Lower Bound	Upper Bound
1	2	.58	.454	.790	-.80	1.97
	3	.02	.454	1.000	-1.37	1.41
	4	-.08	.454	1.000	-1.47	1.30
	5	.69	.476	.695	-.76	2.15
	6	2.49*	.476	.000	1.04	3.95
2	1	-.58	.454	.790	-1.97	.80
	3	-.56	.454	.814	-1.95	.82
	4	-.67	.454	.686	-2.05	.72
	5	.11	.476	1.000	-1.35	1.56
	6	1.91*	.476	.005	.45	3.36
3	1	-.02	.454	1.000	-1.41	1.37
	2	.56	.454	.814	-.82	1.95
	4	-.10	.454	1.000	-1.49	1.28
	5	.67	.476	.721	-.78	2.13
	6	2.47*	.476	.000	1.02	3.93
4	1	.08	.454	1.000	-1.30	1.47
	2	.67	.454	.686	-.72	2.05
	3	.10	.454	1.000	-1.28	1.49
	5	.78	.476	.588	-.68	2.23
	6	2.58*	.476	.000	1.12	4.03
5	1	-.69	.476	.695	-2.15	.76
	2	-.11	.476	1.000	-1.56	1.35
	3	-.67	.476	.721	-2.13	.78
	4	-.78	.476	.588	-2.23	.68
	6	1.80*	.497	.013	.28	3.32
6	1	-2.49*	.476	.000	-3.95	-1.04

2	-1.91[*]	.476	.005	-3.36	-.45
3	-2.47[*]	.476	.000	-3.93	-1.02
4	-2.57[*]	.476	.000	-4.03	-1.12
5	-1.80[*]	.497	.013	-3.32	-.28

Based on observed means.

 The error term is Mean Square(Error) = .618.

*. The mean difference is significant at the .05 level.

Appendix J

Post-hoc Tests for Seeds Recovered in First Eight Searches in the Spatial Associative Learning

Task

Table J1

Post-hoc Bonferroni pairwise comparisons between trials for seeds recovered in first eight searches in the spatial associative learning task. Significance values at or below p = 0.05 are highlighted for visibility.

(I) Trial	(J) Trial	Mean Difference (I-J)	Std. Error	Sig.[b]	95% Confidence Interval for Difference[b]	
					Lower Bound	Upper Bound
1	2	-.361	.174	1.000	-.959	.237
	3	-.272	.249	1.000	-1.129	.584
	4	-.378	.271	1.000	-1.310	.554
	5	-.922	.321	.209	-2.025	.180
	6	-1.089[*]	.288	.020	-2.080	-.098
	7	-1.311[*]	.341	.017	-2.486	-.137
	8	-1.033[*]	.293	.039	-2.040	-.027
2	1	.361	.174	1.000	-.237	.959
	3	.089	.240	1.000	-.736	.914
	4	-.017	.240	1.000	-.843	.810
	5	-.561	.326	1.000	-1.684	.562
	6	-.728	.306	.678	-1.780	.325
	7	-.950	.371	.445	-2.226	.326
	8	-.672	.304	.980	-1.717	.373
3	1	.272	.249	1.000	-.584	1.129
	2	-.089	.240	1.000	-.914	.736
	4	-.106	.210	1.000	-.829	.617
	5	-.650	.294	.983	-1.661	.361
	6	-.817	.256	.096	-1.698	.065
	7	-1.039	.343	.143	-2.218	.140
	8	-.761	.288	.366	-1.751	.229
4	1	.378	.271	1.000	-.554	1.310
	2	.017	.240	1.000	-.810	.843
	3	.106	.210	1.000	-.617	.829

	5	-.544	.237	.817	-1.360	.272
	6	-.711	.283	.497	-1.684	.262
	7	-.933	.341	.294	-2.107	.240
	8	-.656	.296	.975	-1.674	.363
5	1	.922	.321	.209	-.180	2.025
	2	.561	.326	1.000	-.562	1.684
	3	.650	.294	.983	-.361	1.661
	4	.544	.237	.817	-.272	1.360
	6	-.167	.276	1.000	-1.116	.783
	7	-.389	.274	1.000	-1.332	.555
	8	-.111	.278	1.000	-1.069	.847
6	1	1.089*	.288	.020	.098	2.080
	2	.728	.306	.678	-.325	1.780
	3	.817	.256	.096	-.065	1.698
	4	.711	.283	.497	-.262	1.684
	5	.167	.276	1.000	-.783	1.116
	7	-.222	.238	1.000	-1.039	.595
	8	.056	.271	1.000	-.877	.989
7	1	1.311*	.341	.017	.137	2.486
	2	.950	.371	.445	-.326	2.226
	3	1.039	.343	.143	-.140	2.218
	4	.933	.341	.294	-.240	2.107
	5	.389	.274	1.000	-.555	1.332
	6	.222	.238	1.000	-.595	1.039
	8	.278	.233	1.000	-.525	1.080
8	1	1.033*	.293	.039	.027	2.040
	2	.672	.304	.980	-.373	1.717
	3	.761	.288	.366	-.229	1.751
	4	.656	.296	.975	-.363	1.674
	5	.111	.278	1.000	-.847	1.069
	6	-.056	.271	1.000	-.989	.877
	7	-.278	.233	1.000	-1.080	.525

Based on estimated marginal means

*. The mean difference is significant at the .05 level.

b. Adjustment for multiple comparisons: Bonferroni.

Table J2

Post-hoc Tukey's HSD pairwise comparisons between flocks for seeds recovered in first eight searches in the spatial associative learning task.

(I) Flock	(J) Flock	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval Lower Bound	95% Confidence Interval Upper Bound
1	2	-.31	.345	.942	-1.36	.74
	3	.73	.345	.309	-.32	1.78
	4	-.40	.345	.858	-1.45	.66
	5	-.61	.362	.555	-1.71	.50
	6	-.12	.345	.999	-1.18	.93
2	1	.31	.345	.942	-.74	1.36
	3	1.04	.345	.054	-.01	2.09
	4	-.08	.345	1.000	-1.14	.97
	5	-.30	.362	.962	-1.40	.81
	6	.19	.345	.994	-.86	1.24
3	1	-.73	.345	.309	-1.78	.32
	2	-1.04	.345	.054	-2.09	.01
	4	-1.12*	.345	.031	-2.18	-.07
	5	-1.34*	.362	.011	-2.44	-.23
	6	-.85	.345	.165	-1.91	.20
4	1	.40	.345	.858	-.66	1.45
	2	.08	.345	1.000	-.97	1.14
	3	1.13*	.345	.031	.07	2.18
	5	-.21	.362	.991	-1.32	.89
	6	.27	.345	.968	-.78	1.32
5	1	.61	.362	.555	-.50	1.71
	2	.30	.362	.962	-.81	1.40
	3	1.34*	.362	.011	.23	2.44
	4	.21	.362	.991	-.89	1.32
	6	.48	.362	.763	-.62	1.59
6	1	.12	.345	.999	-.93	1.18
	2	-.19	.345	.994	-1.24	.86
	3	.85	.345	.165	-.20	1.91
	4	-.27	.345	.968	-1.32	.78
	5	-.48	.362	.763	-1.59	.62

Based on observed means.

 The error term is Mean Square(Error) = .357.

*. The mean difference is significant at the .05 level.

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Cho, G. H., Sherry, D. F., & Roberts, W. A. (2017, June). Social rank is not correlated with learning ability in black-capped chickadees. Poster session - 54th Annual Conference of the Animal Behavior Society, Toronto, ON.