

August 2012

Social Episodic-Like Memory in the Black-Capped Chickadee (*Poecile Atricapillus*)

Alisha A. Wiechers

The University of Western Ontario

Supervisor

David F. Sherry

The University of Western Ontario

Graduate Program in Neuroscience

A thesis submitted in partial fulfillment of the requirements for the degree in Master of Science

© Alisha A. Wiechers 2012

Follow this and additional works at: <https://ir.lib.uwo.ca/etd>

 Part of the [Psychology Commons](#)

Recommended Citation

Wiechers, Alisha A., "Social Episodic-Like Memory in the Black-Capped Chickadee (*Poecile Atricapillus*)" (2012). *Electronic Thesis and Dissertation Repository*. 726.

<https://ir.lib.uwo.ca/etd/726>

This Dissertation/Thesis is brought to you for free and open access by Scholarship@Western. It has been accepted for inclusion in Electronic Thesis and Dissertation Repository by an authorized administrator of Scholarship@Western. For more information, please contact tadam@uwo.ca, wlsadmin@uwo.ca.

SOCIAL EPISODIC-LIKE MEMORY IN THE BLACK-CAPPED CHICKADEE

(POECILE ATRICAPILLUS)

(Spine title: SOCIAL EPISODIC-LIKE MEMORY)

(Thesis format: Integrated Article)

by

Alisha A. Wiechers

Graduate Program in Neuroscience

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science

The School of Graduate and Postdoctoral Studies
The University of Western Ontario
London, Ontario, Canada

© Alisha A. Wiechers 2012

THE UNIVERSITY OF WESTERN ONTARIO
School of Graduate and Postdoctoral Studies
CERTIFICATE OF EXAMINATION

Supervisor

Dr. David Sherry

Examiners

Dr. Scott MacDougall-Shackleton

Supervisory Committee

Dr. Bill Roberts

Dr. Elizabeth Hampson

Dr. Derek Mitchell

Dr. Mark Cole

The thesis by

Alisha Ann Wiechers

Entitled:

**Social Episodic-like Memory in the
Black-capped Chickadee (*Poecile atricapillus*)**

is accepted in partial fulfillment
of the requirements for the degree of
Master of Science

Date _____

Chair of the Thesis Examination Board

ABSTRACT

Episodic memory is the ability to remember previously experienced past events (Tulving 1992). An important component of episodic memory is auto-noetic consciousness. Auto-noetic consciousness is self-awareness that you personally experienced an event (Tulving 1985). Historically, episodic memory was thought to be a purely human ability but recently episodic memory has been tested in animals by using what-where-when paradigms. Since auto-noetic consciousness is not examined in animals, it is referred to as episodic-like memory.

A social component of episodic-like memory has not previously been examined in animals. The current study modified the what-where-when paradigm to test who and when components of episodic-like memory. In the first experiment, subordinate birds were required to associate a short retention interval (SRI) with the dominant bird being present and a long retention interval (LRI) with the dominant bird being absent. Dominant birds hinder the ability of a subordinate bird to access food. Episodic-like memory of who and when was demonstrated in SRI probe trials in which the dominant bird was absent. Subordinate birds behaved on SRI probe trials as if the dominant bird was present. In Experiment 2, the interval at which the dominant bird appeared was reversed. Subordinate birds behaved on LRI probe trials as if the dominant bird was present, when the dominant bird was actually absent. These results provide evidence for who and when components of episodic-like memory by requiring recollection of how long ago an individual last experienced a social encounter and using this to predict the absence or presence of a dominant bird.

Keywords: Episodic-like memory, what-where-when memory, social behavior, dominance, black-capped chickadee

CO-AUTHORSHIP

Alisha Wiechers performed all research described in this thesis including data collection and data analysis. Alisha Wiechers, Dr. David Sherry and Dr. Miranda Feeney collaborated on the experimental design. Dr. David Sherry supervised editing of the manuscript presented in Chapter 2. Experiment 1 and 2 are original research carried out for this Master's thesis.

ACKNOWLEDGEMENTS

I would like to express my sincere gratitude and appreciation to my supervisor Dr. David Sherry for his invaluable assistance from start to finish of this thesis.

I would like to thank my advisory committee Dr. Bill Roberts, Dr. Scott MacDougall – Shackleton, Dr. Brian Corneil, Dr. Raj Rajakumar, and Dr. Derek Mitchell for their helpful comments and feedback on this project.

Thank you to my fellow researchers in the Sherry lab for all of their expertise and advice throughout this project.

A special thank you to my parents for all their support throughout my education, and to the rest of my family for all their love and encouragement.

Lastly and most importantly, I would like to thank my husband William Booth for everything that he is and everything he has done to help me throughout my Master's Degree.

TABLE OF CONTENTS

Certificate of Examination	ii
Abstract	iii
Co-Authorship.....	iv
Acknowledgements.....	v
Table of Contents	vi
List of Figures	viii
List of Abbreviations and Symbols.....	ix
Chapter 1	1
General Introduction	1
References	9
Chapter 2.....	12
Abstract	13
Introduction.....	14
Experiment 1	17
Methods.....	18
Results.....	22
Discussion.....	24
Experiment 2.....	28
Methods.....	29
Results.....	30
Discussion.....	32
References.....	36
Chapter 3.....	38
General Discussion	38

References.....	45
Figures.....	46
Ethics Approval	57
Curriculum Vitae	59

LIST OF FIGURES

Figure 1	Testing room setup for social testing in Experiment 1 and Experiment 2	46
Figure 2	Social training and testing experimental paradigm for Experiment 1	47
Figure 3	Mean number of worms taken by subordinate birds across trial types	48
Figure 4	Mean number of worms taken by subordinate and dominant birds on LRI training and control trials	49
Figure 5	Mean number of worms taken in Phase 1 by subordinate and dominant birds across trial types	50
Figure 6	Latency to enter room and to take a worm by subordinate birds across trial types	51
Figure 7	Social training and testing experimental paradigm for Experiment 2	52
Figure 8	Mean number of worms taken by subordinate birds across trial types	53
Figure 9	Mean number of worms taken by subordinate and dominant birds on SRI training and control trials	54
Figure 10	Mean number of worms taken in Phase 1 by subordinate and dominant birds across trial types	55
Figure 11	Latency to enter room and to take a worm by subordinate birds across trial types	56

LIST OF ABBREVIATIONS

SRI	short retention interval
LRI	long retention interval
Tukey's HSD	Tukey's Honestly Significant Difference

CHAPTER 1

In 1972, Tulving defined episodic memory as the ability to remember personally-experienced past events. There were three important components to this definition; what occurred during a unique event, when the event took place, and where the event took place. A problem with this definition is that episodic memory can occur without all three components. For example, it is possible to remember going to Paris (where component) and seeing the Eiffel tower (what component) but not remembering exactly when this event took place (when component). It is also possible to have all three components of memory without actually personally experiencing an event. For example, it is possible to know what happened during WWI, know when it happened, and know where it happened but not have personally experienced the event. In 1985, Tulving updated the classic definition of episodic memory to include auto-noetic consciousness. Auto-noetic consciousness is self-awareness which gives rise to remembering in the sense of self-recollection. It is conscious awareness for having personally experienced an event which helps distinguish between remembering and knowing. Knowing is a type of memory known as semantic memory that refers to general knowledge about the world (Tulving 1972). For example, it is possible to know that the Eiffel tower is located in France but to not have gained this knowledge through experience. In contrast, remembering is a type of memory known as episodic memory. This type of memory was personally experienced.

Recent research suggests that animals are capable of episodic memory though it is unclear whether animals are capable of recollecting past events with the same self awareness humans possess for personally experienced events (Clayton and Dickinson 1998; Feeney, Roberts, & Sherry 2009; Zinkivskay, Nazir, & Smulders 2009). Auto-noetic consciousness is tested in

humans through verbal reports of the participant realizing that their memories were personally experienced. Unfortunately, this updated version of episodic memory presents a barrier to examining episodic memory in animals because there are no agreed upon behavioral markers of conscious experience (Clayton and Dickinson, 1998).

One way to partially overcome this problem is to revert back to the classic definition of episodic memory presented by Tulving in 1972. Since auto-noetic consciousness is lacking from this definition, episodic memory in animals when tested with the what-where-when criteria, was called *episodic-like memory* because it lacks the crucial auto-noetic components of episodic memory in humans (Clayton and Dickinson 1998).

There are many examples in nature of animals benefiting from the capacity to remember the what, where, and when components of individual past episodes. For example, food storing birds are capable of caching hundreds of food stores throughout the winter months and retrieving them days, weeks, or even months later (Hoshooley and Sherry 2007; Cowie, Krebs, and Sherry. 1981). The hippocampus, a brain structure necessary for spatial memory, is crucial for accurate cache recovery (Sherry and Vaccarino 1998; Hampton and Shettleworth 1996). Food-storing birds must remember what they cached, where they cached it, and also when they cached the food in order to successfully retrieve their food stores. The animal must be able to encode information based on a single personal experience and accurately recall that information at a later date. Black-capped chickadees (*Poecile atricapillus*) are quite accurate at remembering what their caches contain (Sherry 1984). Chickadees spent relatively more time at and make relatively more visits to cache sites containing their preferred food, compared to cache sites containing their non-preferred food (Sherry 1984). Black-capped chickadees are also quite accurate at remembering where they

stored food in conjunction with what their caches contained and when they encountered this food (Feeney et al. 2009). Considering these results, it seems likely that food-storing birds have what-where-when memory.

Clayton and Dickinson (1998) reported episodic-like memory in scrub jays (*Aphelocoma coerulescens*) using a what, where, when paradigm. Scrub jays are food-storing corvids that cache both perishable and non-perishable food. In a sand-filled ice-cube tray, scrub jays cached preferred but perishable wax worms and less preferred non-perishable peanuts. Either 4 hours or 124 hours after caching, memory was tested by presenting the birds with the same tray. Peanuts were still palatable 4 hours and 124 hours later, but the wax worms were palatable only after the 4 hour delay period. After 124 hours, the wax worms were degraded making them unpalatable. Eventually the scrub jays learned to search the worm locations prior to the peanut locations after the 4 hour delay period and learned to search the peanut locations before the worm locations after the 124 hour delay period. This differential recovery preference of scrub jays demonstrated that the birds were able to learn to associate a short retention interval (SRI) with the worms still being fresh and a long retention interval (LRI) with the worms being degraded. This study also demonstrates that the birds could remember where food was located, what type of food was in the cache, and when the caching episode had taken place. This experiment successfully demonstrated what-where-when episodic-like memory in scrub jays.

Feeney et al. (2009) were able to demonstrate what-where-when memory in black-capped chickadees, another species of food-storing birds. They designed a paradigm similar to Clayton and Dickinson (1998) which used meal worms and sunflower seeds as the what-component, locations in trees as the where-component, and different retention intervals as the

when-component. If chickadees were able to differentially search for food rewards based on how long the interval was between search phases, they would demonstrate what, where, and when memory. In the first phase of the experiment chickadees searched for hidden sunflower seeds and mealworms in trees located in an indoor aviary. In the second phase, birds returned to the observation room after either an SRI of 3 hours or an LRI of 123 hours. After an SRI, both the seeds and worms were palatable. After an LRI, the seeds were still palatable but the worms had been chemically degraded making them inedible. The results from this experiment showed that the birds searched in worm locations first, significantly more often during SRI trials than during LRI trials. They searched the worm locations first, more often on SRIs when the worms were palatable and fresh than they did on LRIs when the worms were degraded and unpalatable. These results demonstrate that chickadees are capable of remembering what, where, and when properties of the food they had previously encountered.

Bird et al. (2003) tested what, where, and when memory in rats using spatial memory for food cached on the radial maze. In this study, rats were allowed to hide food in an 8- arm radial maze by taking food from the center of the maze to boxes at the end of each arm. After rats had hidden four items, they were tested for retrieval. These tests showed that the rats selectively returned to the maze arms where they had hidden food. Rats have a preference for cheese over pretzels and when they were allowed to hide both, they returned to the arms baited with cheese prior to returning to the arms baited with pretzels. These experiments clearly indicated a memory for what and where. In another experiment examining what, where, and when memory, rats were able to choose between arms baited with cheese and pretzels. At a one hour delay interval the cheese was fresh but at a 25 hour

delay interval the cheese was degraded. The concept behind this experimental setup is that if the rats are able to associate a certain time interval with degraded cheese and another time interval with fresh cheese, they should preferentially search the arms baited with cheese on the 1 hour interval but not the 25 hour interval. The data showed no preference for the pretzel arm on trials with a 25 hour delay interval when the cheese was degraded. Results from this experiment demonstrated what and where memory in rats but failed to demonstrate a when component.

A study examining what, where, and when memory in rats demonstrated that rats were able to remember in detail, what happened during an event, in addition to when and where the event occurred (Babb and Crystal 2006). This experiment used an 8-arm radial maze to provide rats with access to two distinctive flavored foods or one non-distinctive flavored food. Locations with distinctive-flavored foods were replenished after a long delay but not after a short delay, while non-distinctive flavored locations were never replenished. Rats were more likely to visit distinctive-flavored locations after a long delay than a short delay demonstrating that they remembered when and where they had recently encountered the distinctive pellets. Afterwards, one distinctive flavor was devalued by pre-feeding that specific flavor or pairing the flavor with lithium chloride to create an acquired taste aversion. After a distinctive flavor was devalued, rats decreased the number of visits to the devalued distinctive flavor but not to the non-devalued distinctive flavor suggesting that rats are able to encode episodic-like memories (Babb and Crystal 2006).

Another study using an 8-arm radial maze and an acquired taste aversion was used to test what, where, and when memory in rats (Babb and Crystal 2005). In this experiment rats were able to visit four preselected arms, one of which provided chocolate pellets. After an

SRI, only the four arms not available in the first phase of the experiment were available. After an LRI, all eight arms were available and the chocolate arm was replenished. The rats made more visits to the arm containing chocolate after an LRI than an SRI. In the next part of this experiment, the chocolate was paired with lithium chloride to create an acquired taste aversion. On the LRI trials, rats made fewer visits to the arm containing chocolate after the lithium chloride treatment than compared to the first part of this experiment. These results could not have been obtained without the rats acquiring knowledge of what, where, and when properties of the food they encountered (Babb and Crystal 2005).

Episodic-like memory has subsequently been tested in many different species such as scrub jays (Clayton and Dickinson 1998), magpies (*Pica pica*) (Zinkivskay et al. 2009), pigeons (*Columba livia*) (Skov-Rackette, Miller, & Shettleworth 2006), mice (*Mus musculus*) (Dere, Huston, & De Sousa 2005), meadow voles (*Microtus pennsylvanicus*) (Ferkin, Combs, del Barco-Trillo, Pierce, & Franklin 2008), gorillas (*Microtus pennsylvanicus*) (Schwartz et al. 2005), and rhesus monkeys (*Macaca mulatta*) (Hampton et al. 2005) with different species supporting or contesting the concept of episodic-like memory in animals.

The crucial component of all these episodic-like or what-where-when experiments is that to solve the task, animals must recall their recent experience with the task and recollect when it occurred, what took place, and where it happened.

A logical extension to current ideas about episodic-like memory in animals is the inclusion of a social component. Many animals are group-living which naturally causes social interaction. Dominance hierarchies, for example, mediate social interactions in many group-living animals, many animals have social relationships, form alliance relationships for resources, or compete for resources. It is likely that if animals live in groups, they are

capable of “who” memory as they come into contact with the same individuals on a regular basis. The memory-based hypothesis of dominance relationships suggests that they are maintained based on memory for previous encounters with a specific individual (Landau 1951a). Support for this hypothesis comes from studies in chickens that have shown upon first encounters, individuals are highly aggressive to one another but decrease their aggressiveness to the same individual in subsequent encounters (Guhl 1968). In jungle crows, dominance is maintained by memories of past encounters with a specific individual, implying individual recognition (Izawa and Watanabe 2008). In contrast, the individual characteristics hypothesis suggests that dominance relationships are determined by individual characteristics such as body size, sex, or age that are reassessed upon each encounter with an individual, even if previously exposed to the same individual (Landau 1951b).

An interesting general question in animal cognition is thus whether animals can form episodic-like recollection involving other individuals. It seems intuitive that they can, considering many are group-living species, but this area of animal memory has not been thoroughly examined.

One study examined the social component of food-caching in Western scrub jays (*Aphelocoma californica*) (Dally, Emery, & Clayton 2006). Scrub jays are food-caching species that hide food for future consumption, steal caches from other animals, and have tactics to minimize the chances of their own caches being pilfered (Dally et al. 2006). In this experiment, scrub jays cached in two ice cube trays, one near an observing bird and one further away from an observing bird. They cached in four conditions: in private, or in the presence of a dominant, subordinate, or partner bird. Three hours later they were permitted to recover their caches in private. The results showed that when the birds cached in view of a

dominant or subordinate bird they were more likely to cache in the far tray than when they cached in private or in partner conditions. They also found that the greatest number of re-caches occurred in the dominant condition – the caching bird moved seeds from the near tray to the far tray. This suggests that scrub jays remembered which individual was watching them and altered their re-caching behavior accordingly. This experiment did not, however, examine whether scrub jay memory for social encounters had a who and when component comparable to the who-what-when components of episodic-like recollection.

Chickadees spend the non-breeding part of their annual cycle in flocks with linear dominance hierarchies based on age, sex, seniority, size, condition, plumage, and vocalizations (Ekman 1989; Lundborg and Borden 2003; Ratcliffe et al. 2007). Black-capped chickadees are flock-living species and have demonstrated what, where, and when memory in past experiments (Feeney et al. 2009).

In the present study, I investigated whether black-capped chickadees are capable of remembering who and when in an episodic-like fashion. The experimental design followed the usual what-where-when design but instead of remembering what kind of food was cached where and when, chickadees were tested to determine if they could recall a recent social interaction and recollect who had been present and when.

References

- Babb, S. J. & Crystal, J. D. (2005). Discrimination of what, when, and where: Implications for episodic-like memory in rats. *Learning and Motivation*, 26, 177-189.
- Babb, S. J. & Crystal, J. D. (2006). Episodic-like memory in the rat. *Current Biology*, 16, 1317-1321.
- Bird, L.R., Roberts, W.A., Abroms, B., Kit, K. A., & Crupi, C. (2003). Spatial memory for food hidden by rats (*Rattus norvegicus*) on the radial maze: Studies of memory for where, what, and when. *Journal of Comparative Psychology*, 117(2), 176-187.
- Cowie, R. J., Krebs, J. R., & Sherry, D. F. (1981). Food storing by marsh tits. *Animal Behavior*, 29, 1252-1259.
- Clayton, N. S., & Dickinson, A. (1998). What, where, and when: episodic-like memory during cache recovery by scrub jays. *Nature*, 395, 272-274. doi: 10.1159/000096984
- Dally, J. M., Emery, N. J., & Clayton, N. S. (2006). Food-caching western scrub-jays keep track of who was watching when. *Science*, 312, 1662-1665.
- Dere E., Huston, J. P. & De Sousa M. A. (2005). Episodic-like memory in mice: simultaneous assessment of object, place, and temporal order memory. *Brain Research Protocols*, 16, 10-19.
- Ekman, J. (1989). *Ecology of non-breeding social systems of Parus*. *Wilson Bulletin*, 101, 263-288.

- Feeney, M.C., Roberts, W. A., & Sherry, D. F. (2009). Memory for what, where, and when in the black-capped chickadee (*Poecile atricapillus*). *Animal Cognition*, *12*, 767-777.
doi:10.1007/s10071-009-0236-x
- Ferkin M. H., Combs A., del Barco-Trillo J., Pierce A. A. & Franklin S. (2008). Meadow voles, *Microtus pennsylvanicus*, have the capacity to recall the “what”, “where”, and “when” of a single past event. *Animal Cognition*, *11*, 147-159.
- Guhl, A.M., 1968. Social inertia and social stability in chickens. *Animal Behavior*, *16*, 219–232.
- Hampton, R. R., & Shettleworth, S. J. (1996). Hippocampus and Memory in a Food-Storing and in a Non-storing Bird Species. *Behavioral Neuroscience*, *110*(5), 946-964.
- Hampton R., Hampstead B., & Murray E. (2005). Rhesus monkeys (*Macaca mulatta*) demonstrate robust memory for what and where but not when, in an open-field test of memory. *Learning and Motivation*, *36*, 245-259.
- Hoshooley, J. S., & Sherry, D. F. (2007). Greater hippocampal neuronal recruitment in food-storing than in non-food-storing birds. *Developmental Neurobiology*, *67*(4), 406-414.
- Izawa, E., & Watanabe, S. (2008). Formation of linear dominance relationship in captive jungle crows (*Corvus macrorhynchos*): Implications for individual recognition. *Behavioral Processes*, *78*(2008), 44-52.
- Landau, H.G. (1951a). On dominance relations and the structure of animal societies. Part II. Some effects of possible social factors. *Bulletin of Mathematical Biophysics*, *13*, 245–262.

- Landau, H.G. (1951b). *On dominance relations and the structure of animal societies. Part I. Effect of inherent characteristics*, 13, 1–19.
- Lundborg, K. & Brodin, A. (2003). The effect of dominance rank on fat deposition and food hoarding in the willow tit *Parus montanus* – an experimental test. *Ibis*, 145, 78-82.
- Ratcliff, L. Mennill, D. J., & Schubert, K. A. (2007). *Reproductive ecology, evolution, and behavior*. In K. A. Otter (Eds.), *Ecology and behavior of chickadees and titmice an integrated approach* (pp. 137-141). New York, NY: Oxford University Press.
- Schwartz B. L., Hoffman M. L., & Evans S. (2005). Episodic-like memory in a gorilla: a review and new findings. *Learning and Motivation*, 36, 226-244.
- Sherry, D. F. (1984). Food storage by black-capped chickadees: Memory for location and contents of caches. *Animal Behavior*, 32(2), 451-464.
- Sherry, D.F., & Vaccarino, A.L. (1998). Hippocampus and memory for food caches in black-capped chickadees. *Behavioral Neuroscience*, 103, 308-318.
- Skov-Rackette S.I., Miller, N. Y., & Shettleworth S. J. (2006). What-where-when memory in pigeons. *Journal of Experimental Psychology Animal Behavior Processes*, 32, 345-358.
- Tulving, E. (1972). *Episodic and semantic memory*. In: *Tulving: E, Donaldson W (eds), Organization of memory*. (pp. 381-398). Academic, San Diego.
- Tulving, E. (1985). How many memory systems are there? *American Psychologist*, 40, 385-398.
- Zinkivskay, A., Nazir F., & Smulders TV (2009). What-where-when memory in magpies (*Pica pica*). *Animal Cognition*, 12, 119-125.

CHAPTER 2

SOCIAL EPISODIC-LIKE MEMORY IN THE BLACK-CAPPED CHICKADEE (*POECILE ATRICAPILLUS*)

Alisha A. Wiechers, Miranda C. Feeney, & David F. Sherry
Western Ontario

Prepared for submission to:
Animal Cognition

ABSTRACT

The social component of episodic-like memory has not previously been examined in animals. The current study used a variation of the what-where-when paradigm to test who and when components of episodic-like memory. In Experiment 1, subordinate birds learned to associate a short retention interval (SRI) with the presence of a dominant bird and a long retention interval (LRI) with the dominant bird's absence. The presence of the dominant bird restricted subordinate birds' access to a preferred food type. Episodic-like recollection of who and when was shown in SRI probe trials in which the dominant bird was absent. Subordinate birds behaved on SRI probe trials as if the dominant bird was present. In a second experiment, the interval at which the dominant bird appeared was reversed. Subordinate birds behaved on LRI probe trials as if the dominant bird was present. These results provide evidence that chickadees were able to recollect in an episodic-like fashion when a prior social encounter had occurred and whether a dominant individual was present or absent.

Keywords: Episodic-like memory, what-where-when memory, social behavior, dominance, black-capped chickadee

Episodic memory is the ability to remember personally experienced past events (Tulving 1972). In 1985, this definition was updated to include auto-noetic consciousness (Tulving 1985). Auto-noetic consciousness is the ability to mentally place ourselves in the past and recollect what we personally experienced in a past event (Tulving 1985). Episodic-memory was once thought to be exclusive to humans but has recently been examined in animals. This ability has been studied in animals using a what-where-when paradigm and has been labeled as episodic-like memory because it lacks the auto-noetic consciousness component of episodic memory (Clayton and Dickinson 1998, Feeney et al. 2009).

The what-where-when paradigms used in food-storing birds made use of food palatability to test birds' ability to search for food after different retention intervals. Food quality changes depending on the retention interval which in turn caused birds' to change their food foraging preference. For example, Feeney et al. (2009) used the what-where-when paradigm with black-capped chickadees. Chickadees searched for sunflower seeds and meal worms hidden on different sides of an indoor aviary. Birds revisited these sites after a short retention interval (SRI) of 3 hours or a long retention interval (LRI) of 123 hours. Chickadees have a strong preference for meal worms over sunflower seeds. After 3 hours, the meal worms were fresh and palatable, but after 123 hours the meal worms were chemically degraded making them no longer palatable. Chickadees showed evidence of what-where-when memory by searching the worm side of the aviary first more often on short 3 hour trials when the meal worms were fresh and palatable than on long 123 hour trials when the meal worms were degraded and unpalatable.

A possible "who" component of episodic-like memory has not been thoroughly examined in animals even though many are group living species. The closest approach to the what-

where-when paradigm was an experiment by Dally et al. (2006) that examined social memory in the Western scrub jay, a food-storing corvid. In this experiment, birds had use of two trays in their home cage to store food either while being observed by another jay or in private. These trays were located either near or far from the observing bird. The observing bird was either a dominant bird, a subordinate bird, or a partner of the storing bird. Three hours after the storing episode, the storing bird was able to re-cache its food stores in private with no observing bird. Results from this study showed that the storing bird re-cached its food most often when a dominant or subordinate bird had been observing them cache food originally as opposed to their partner bird or no observer. These results suggest that scrub jays are able to remember who watched them store their food and alter their re-caching behavior accordingly (Dally et al. 2006). This experiment did not, however, attempt to test whether recollection of recent social experience met the what-where-when criteria of episodic-like memory. Although caching birds' behavior was affected by who had observed them, a variety of mechanisms could produce this effect, including tagging of caches in memory as safe or vulnerable.

Black-capped chickadees are an ideal species for examination of who and when memory. They are a social, group-living species that lives in the same small geographical area throughout their life (Smith 1991). This means that chickadees encounter the same individuals throughout their entire adult life. In the winter months, chickadees live in flocks of up to twelve birds including both male and female adults and juveniles (Smith 1991). The flock structure is mediated by a dominance hierarchy formed through interactions at feeding sites (Smith 1991). The dominance hierarchy is based on age, sex, seniority, size, condition, plumage, and vocalizations (Ekman 1989; Lundborg and Brodin 2003). The dominance-

forming interactions consist of conspicuous, aggressive behavior such as supplanting, chasing, gaping, ruffling of crown feathers, and ruffling of body feathers (Ekman 1989).

Because chickadees are a social, group-living species with a clear linear dominance hierarchy, I used dominance relations to test for a social component of episodic-like memory.

The current experiment used a modified what-where-when paradigm to test who and when memory in black-capped chickadees. Subordinate birds learned a dominant bird would be present or absent based on an elapsed retention interval. The “who” component of this experiment was whether the dominant bird was present or absent and the “when” component was the length of the retention interval. This paradigm is similar to what-where-when studies that manipulate the palatability of food over time but uses the presence of a dominant bird rather than deterioration of a preferred food as the variable that changes in relation to the retention interval.

This experiment tested for episodic-like memory by requiring birds to remember when they last experienced a social encounter in Phase 1 of the trials in order to accurately predict the nature of their next encounter in the second phase of the trial. In order to correctly predict whether the dominant bird will be absent or present, they must have some recollection of when their previous encounter with this bird occurred. Chickadees’ ability to remember who and when adds a social component to episodic-like memory in black-capped chickadees.

EXPERIMENT 1

Purpose

Experiment 1 tested episodic-like memory in black-capped chickadees, specifically when components. Subordinate birds were trained to associate an SRI trial with a dominant bird being present and an LRI trial with the dominant bird being absent. This procedure was used to mimic a natural situation in which if a subordinate bird sees a dominant bird at a feeder, it is likely that the dominant bird will still be present after a short period but absent after a long period. During probe trials, the dominant bird was not present after the SRI. If the subordinate birds are able to learn an association between the dominant birds and a short retention interval, then during the probe trials the subordinate birds should act as though the dominant bird is present even though it is actually absent. Thus, probe trials examined the subordinate birds' behavior when the dominant bird was absent, compared to their behavior on the training trials when the subordinate bird was actually present. This task was designed to test episodic-like memory by requiring the subordinate birds to learn when they last encountered the dominant bird. Although the subordinate birds likely made use of interval timing to distinguish SRIs from LRIs, the design has the same episodic-like memory criteria as standard what-where-when experiments. The subordinate bird had to recall its previous social encounter and recollect when that occurred.

Methods

Subjects

Subjects were 10 adult black-capped chickadees (*Poecile atricapillus*) used in a previous behavioral experiment. The birds were maintained on a Mazuri Diet (PMI Nutrition International LLC, Brentwood, MO, USA) mixed with raw hulled sunflower seeds and peanuts that was freely available at all times in the home cage. These ingredients were ground to a fine powder to prevent the birds from caching food in their home cages. Water was also available at all times. Birds were individually housed in their home cages in a common holding room with other chickadees and tested in an indoor aviary. Birds were housed, tested, and observed through a three-part observation suite. The holding room, testing room, and observation room were adjoined allowing birds to enter the testing room from their home cage through an automatic door. Birds were observed in the testing room through a one way mirror connecting the testing room and observation room. Birds were maintained on a 10/14 hour light/dark cycle with light onset at 7 a.m. Birds held in captivity under an Environment Canada Scientific Capture permit and were treated in accordance with the requirements of the University of Western Ontario Animal Use Subcommittee and the Canadian Council on Animal Care.

Materials

Dominance Testing

The indoor aviary contained two perches and one food platform. A food dish containing 12 raw hulled sunflower seeds and a water dish was located on the food platform.

Social Testing

The indoor aviary contained two perches and two food platforms raised 92 cm above the ground, see Figure 1. A shield 37 cm in height surrounded each platform on three sides such that a bird could not see if the other bird was feeding at the platform without approaching and while feeding could not see the other bird until that bird approached. The open non-shielded side of the platform faced the observer. Each food platform contained a bowl of either 12 raw hulled sunflower seeds or 12 small meal worms and a water dish.

On all trials, behavior was recorded on a Noldus Observer X software program.

Procedure

Dominance Testing

Birds were sorted into pairs over the course of three dominance trials. Two birds were put into the indoor aviary for a 5 minute trial. Dominance behavior was observed and recorded for both birds for the complete trial. Once the trial was complete, the birds were placed back into their home cages. After 1 hour, another dominance trial occurred. Supplant, when a dominant bird displaces a subordinate bird from a perch, proved to be the most useful dominance behavior as all dominant birds repeatedly supplanted the subordinate bird, but no subordinate bird ever supplanted a dominant bird. A dominance pair was established if one bird exclusively supplanted the other bird at least once on each of the three trials. Once a dominance pair was established, they remained paired together throughout the entire experiment.

Social Testing

Training

Training trials during the experiment consisted of two phases, see Figure 2. Phase 1 began at different times throughout the day to avoid time-place learning. At the start of Phase 1, a dominant-subordinate bird pair were permitted to enter the indoor aviary for 5 minutes. Once a bird left its home cage and entered the testing room, the door to its cage was closed to stop the bird from reentering its home cage. Throughout the trial, behavior was observed and recorded for both the dominant and subordinate bird. These behaviors recorded were enter room and take worm. Once 5 minutes elapsed, both birds were put back into their home cages.

Phase 2 commenced after either a short retention interval (SRI) or a long retention interval (LRI). On an SRI trial, 10 minutes after Phase 1 was complete both birds were put back into the indoor aviary for another 5 minute trial. Both sunflower seeds and meal worms were replenished for each trial and the same behaviors were observed and recorded for each bird. On an LRI trial, 1 hour after Phase 1 was complete, only the subordinate bird was returned to the indoor aviary with access to meal worms and sunflower seeds. Behavior was observed and recorded for the subordinate bird for the 5 minute trial. Once Phase 2 was complete, the birds were returned to their home cages.

Bird pairs experienced a single trial once a day, five days a week for a total of 15 LRI and 15 SRI trials. A schedule was generated that randomized whether the birds received an SRI or LRI trial. The purpose of the training trials was to have the subordinate bird learn when a

dominant bird would be present or absent. They should learn to associate an SRI with the dominant bird being present and an LRI trial with the dominant bird being absent.

Probe and Control Trials

After the birds completed 30 training trials, three SRI probe trials followed by three LRI control trials were conducted. These trials were interspersed among additional training trials. On probe trials, the interval at which the dominant bird appeared was changed from the training trials, see Figure 2. On SRI probe trials, Phase 1 was as during the SRI training trials, but during Phase 2, which followed Phase 1 by 10 minutes, only the submissive bird was allowed into the testing room for 5 minutes with access to meal worms and sunflower seeds.

On LRI control trials, Phase 1 was as during LRI training trials, but during Phase 2, which followed Phase 1 by 60 minutes, only the dominant bird was allowed into the testing room for 5 minutes with access to meal worms and sunflower seeds.

LRI control trials were also conducted to examine how a bird would behave as a function of the 1 hour interval between Phase 1 and 2. This trial provided additional information on the dominant birds' behavior after an LRI that was then compared to the behavior of a subordinate bird after the LRI training trials. This trial specifically provided data on whether food consumption increases after an LRI as a function of how long ago the bird had access to worms rather than any association between retention intervals and the presence of dominant birds.

Each pair of birds completed three SRI and three LRI control trials. The probe and control trials were placed intermittently within the randomized training schedule. Before a

subsequent probe or control trial was conducted, the birds experienced a training trial of the same retention interval to refresh the birds' memory of the training paradigm. SRI probe trials were conducted first, followed by LRI control trials.

Results

Subordinate birds

A repeated measures analysis of variance was used to compare the mean number of worms taken by subordinate birds across SRI training trials, LRI training trials, and SRI probe trials. Subordinate birds took significantly different numbers of worms on the LRI training trial, SRI training trial, and SRI probe trial, $F(2, 8) = 13.25$, $p < .05$, see Figure 3.

Tukey's HSD indicated that subordinate birds took more worms on the LRI training trial than on either the SRI training trial ($q(3, 8) = 9.76$, $p < .05$) or SRI probe trial ($q(3, 8) = 9.76$, $p < .05$). These results suggested that the subordinate bird had come to associate an SRI trial with the dominant bird being present and took fewer worms. Subordinate birds had learned to associate an LRI training trial with the dominant bird being absent and took more worms than when the dominant bird was present. On the SRI probe trial, the subordinate bird acted as though the dominant bird was present by taking a similar number of worms as on an SRI training trial.

Dominant vs. Subordinate bird – LRI

An independent t-test was used to compare the mean number of worms taken by the dominant bird on the LRI control trials and the subordinate bird on the LRI training trials. Subordinate birds took more worms on LRI training trials than dominant birds took on the LRI trials, $t(8) = 3.76$, $p < .01$, see Figure 4.

Subordinate vs. Dominant bird – Phase 1

The mean number of worms taken by dominant and subordinate birds during Phase 1 was compared for each trial type using an independent t-test for each comparison. On the SRI training trials, dominant birds ate a similar number of worms to those eaten by subordinate birds in Phase 1, $t(8) = .46$, *ns*, see Figure 5a. On the LRI training trial, dominant birds ate a similar number of worms as those eaten by subordinate birds in Phase 1, $t(8) = 0.74$, *ns*, see Figure 5b. Dominant birds ate a similar number of worms as those eaten by subordinate birds in Phase 1 of the SRI probe trials, $t(8) = 1.35$, *ns* see Figure 5c. Dominant birds ate a similar number of worms as subordinate birds in Phase 1 of the LRI control trials, $t(8) = 1.55$, *ns* see Figure 5d.

Latency to Enter Room

The latency for the subordinate bird to enter the room from the start of the trial was compared across SRI training, LRI training, and SRI Probe trials with a repeated measures analysis of variance.

Results indicate that subordinate birds entered the room at a similar time on SRI training trials, LRI training trials, and SRI probe trials, $F(2, 8) = 1.56$, *ns*, see Figure 6a.

Latency to Take Worm

The latency from the start of the trial for the subordinate bird to take a worm was compared across SRI training, LRI training, and SRI probe trials with a repeated measures analysis of variance.

Results indicate that subordinate birds took their first worm at a similar time on SRI training trials, LRI training trials, and SRI probe trials, $F(2, 8) = 1.56$, *ns*, see Figure 6b.

Discussion

It was hypothesized that a subordinate black-capped chickadee would be able to learn that a dominant bird will be present after a short retention interval but absent after a long retention interval. The results from this study indicate that subordinate birds are able to remember when a dominant bird is supposed to be present and act accordingly. These results were inferred through measures of number of worms taken. Subordinate birds behaved on SRI probe trials as if the dominant birds were still present though they were actually absent. Subordinate birds took a similar number of worms on the SRI training and SRI probe trials, less than on the LRI training trials when they had learned the dominant bird would be absent.

It was hypothesized that black-capped chickadees may be able to remember who and when because of the selective advantage these traits confer to animals that live in social and food-storing environments. Previously black-capped chickadees were shown to be able to remember what, when, and where while performing a food-storing task (Feeney et al. 2009). Since chickadees form flocks in the winter months with structure based on dominance ranking (Ratcliffe et al. 2007), it was hypothesized that chickadees will also be able to remember who in conjunction with what and when. As expected, I found that chickadees were able to remember when they had encountered a dominant individual.

Subordinate birds took more worms on the LRI trials when the subordinate bird was alone than on either SRI trials when the dominant bird was present or on SRI probe trials when the dominant bird was absent but supposed to be present. These results suggest that the

subordinate birds had learned to associate the short retention interval with the dominant bird being present. Even on the probe trials, the subordinate bird acted as though the dominant bird was present and took fewer worms. It is interesting that even though the dominant bird was visually absent, the subordinate bird still acted as though the dominant bird was present. This is in contrast to the LRI, when the subordinate bird had learned the dominant bird would be absent and took significantly more worms than on the SRI trials. These results suggest that the subordinate birds have learned that they will be alone after an LRI with free access to the meal worms. Based on these results, it can be suggested that subordinate birds were able to learn a who and when association between retention intervals and the presence of a dominant bird. These results provide support for evidence of episodic-like memory in black-capped chickadees.

In order to control for interval length, I compared the mean number of worms taken on LRI trials for both dominant and subordinate birds to see whether the subordinate birds were taking more worms on the LRI training trials simply as a function of longer interval length rather than knowing that the dominant bird would be absent. If subordinate birds took more worms on LRI trials than SRI trials merely because more time had elapsed since their last encounter with meal worms, I would expect to see both the dominant birds and subordinate birds taking more worms on the LRI trials than the SRI trials. The results do not support the interval length prediction. Dominant birds exposed to the same interval length did not take more worms on LRI control trials. In fact, subordinate birds took more worms than the dominant birds on LRI trials. This is probably due to a motivational effect in the subordinate bird. Perhaps when the subordinate bird has learned that it will be alone, it takes full advantage of free access to the meal worms without hindrance by the dominant bird.

I also measured the number of worms taken in Phase 1 across all trial types by both the dominant and subordinate birds to ensure that the dominant birds were not filling themselves up with worms during Phase 1, and therefore taking fewer worms than the subordinate bird in the LRI control trials described above. As indicated by the results, the subordinate birds were able to gain access to the meal worms during Phase 1 and took a similar number of worms across trial types. It is important to note that the birds were not food deprived prior to or during the experimental procedure which adds support to the suggestion that the subordinate birds took more worms than the dominant birds on the LRI control trials not as a function of hunger, but from having learned the dominant bird would be absent and they would have access to the meal worms without interference by the dominant bird.

Latency to take a worm was also analyzed for the subordinate bird. The reasoning behind this measure is that upon observation of the training and probe trials, subordinate birds appeared to wait for the dominant bird to feed prior to attempting to take a meal worm for itself. Results from this measure indicate that subordinate birds took their first worm at a similar time across trial types. Subordinate chickadees were not quicker to take a worm when they were alone as opposed to when the dominant bird was present.

Latency to enter the room was examined to see whether subordinate birds took longer to enter the testing room when the dominant bird was or was not supposed to be present.

Results from this analysis show that subordinate birds did not take longer to enter the room on SRI training or SRI probe trials than on LRI training trials. Across all types of trials, the subordinate birds entered the room at approximately the same time. Therefore, the finding that subordinate birds took more worms on the LRI trials (when the dominant bird was

supposed to be and was absent) cannot be attributed to entering the room sooner on LRI trials.

The results from this study suggest that black-capped chickadees are capable of remembering who, in conjunction with when. This paradigm was designed to mimic a situation that a chickadee would encounter in the wild. If a subordinate bird sees a dominant bird present at a food source, it is likely that the dominant bird will still be present after a short interval but more likely the dominant bird will be absent from the food source after a long interval.

This experiment requires the birds to remember when they experienced their last Phase 1 episode in order to anticipate the presence or absence of a dominant bird in Phase 2.

Episodic memory is the ability to remember personally experienced past events (Tulving 1972). Birds must recollect that they experienced Phase 1 either a short time or a long time ago. If birds recollect experiencing Phase 1 a short time ago, they can anticipate the dominant bird being present and act accordingly. If the birds recollect that they experienced Phase 1 a long time ago, they can anticipate the dominant bird being absent and therefore having free access to the meal worms and act accordingly. In reference to Tulving's definition of episodic memory (Tulving 1972), this experiment requires the birds to remember how long ago they personally experienced a Phase 1 trial. These results support the existence of episodic-like memory in the black-capped chickadee because the birds appear to recollect whether their most recent Phase 1 episode occurred a short time or a long time ago.

This experiment provides evidence for who and when memory in the black-capped chickadee based on the anticipation of a dominant bird to be present or absent. This learned association is important for providing an original contribution to Tulving's definition of episodic-like

memory in animals (Tulving 1972). Specifically, this adds a “who” component in chickadees to the former what, where, when components of episodic-like memory.

It is possible, however, that the results of this experiment are confounded with the passage of time. Subordinate birds took more worms after a long interval than after a short interval.

Another explanation might be stress levels of the subordinate bird. It is possible that subordinate birds are stressed after an encounter with dominant birds during Phase 1, and therefore take more worms on Phase 2 of an LRI than Phase 2 of an SRI because their stress levels have decreased during the long retention interval. Though this stress explanation is possible, research on the effects of social stress, in particular the presence of a dominant bird, on eating behavior is rare. Nevertheless, there may be other unknown factors that continue to affect the behavior of the subordinate bird on SRI probe trials shortly after its encounter with a dominant bird that cease to affect its behavior on LRI trials purely as a function of passage of time. The most direct way to test if this is to reverse the time interval relations such that subordinates do not re-encounter the dominant after an SRI but instead re-encounter the dominant following an LRI. This was the procedure for Experiment 2.

EXPERIMENT 2

Purpose

Experiment 2 tested who-when memory in black-capped chickadees using the same paradigm as Experiment 1, but the intervals at which the dominant bird appears were reversed. This change not only controlled for passage of time effects that might have produced different behavior after SRIs and LRIs but also tested the birds’ ability to make who-when associations when the associations are contradictory to naturalistic situations. The

results from Experiment 1 suggest that subordinate birds remember when the dominant bird is supposed to be present and act as though it is present on probe trials (when it is actually absent). Experiment 2 controlled for these time-related alternative explanations by reversing the time intervals at which the dominant bird appeared.

Methods

Subjects

Subjects were ten adult black-capped chickadees (*Poecile atricapillus*) not used in Experiment 1. They were caught from the wild between mid-August, 2011 and mid-September, 2011 in London, Ontario.

Materials

Dominance testing and social testing in Experiment 2 used the same apparatus as described for Experiment 1.

Procedure

Social Testing

Training

The training procedure as in Experiment 2 was the same in Experiment 1 except with the retention intervals reversed, see Figure 7. On an SRI trial, 10 minutes after Phase 1 was complete only the subordinate bird was returned to the indoor aviary with access to meal worms and sunflower seeds for another 5 minute trial. On an LRI trial, 1 hour after Phase 1 was complete; both birds were put back into the indoor aviary with access to meal worms and sunflower seeds.

The purpose of the training trials was to have the subordinate bird learn when a dominant bird would be present. They were expected to associate an SRI with the dominant bird being absent and an LRI trial with the dominant bird being present.

Probe and Control Trials

Probe and control trials were similar to the probe and control trials used in Experiment 1 except with the retention intervals switched.

For Phase 2 of an LRI probe trial, only the subordinate bird was put into the testing room one hour after Phase 1 was complete with access to meal worms and sunflower seeds, as compared to Phase 1 when both the subordinate and dominant bird were in the testing room. For Phase 2 of SRI control trials, 10 minutes after Phase 1 was complete, only the dominant bird was put back into the testing room with access to meal worms and sunflower seeds, as compared to Phase 1 when only the subordinate bird was in the testing room.

Results

Subordinate birds

A repeated measures analysis of variance was used to analyze the mean number of worms taken by subordinate birds across SRI training trials, LRI training trials, and LRI probe trials. Subordinate birds took significantly different numbers of worms on the SRI training trial, LRI training trial, and LRI probe trial, $F(2, 8) = 22.88$, $p < .001$, see Figure 8.

Tukey's HSD indicated that subordinate birds took more worms on the SRI training trial than on either the LRI training trial ($q(3, 8) = 6.01$, $p < .05$ or LRI probe trial ($q(3, 8) = 8.14$, $p < .05$). These results suggest that the subordinate bird had come to associate an LRI trial with

the dominant bird being present and took fewer worms. Subordinate birds had learned to associate an SRI training trial with the dominant bird being absent and took more worms than when the dominant bird was present. On the LRI probe trial, the subordinate bird acted as though the dominant bird was present by taking a similar number of worms as on an LRI training trial.

Dominant vs. Subordinate bird – LRI

An independent t-test was used to compare the mean number of worms taken by the dominant bird on the SRI control trials and the subordinate bird on the SRI training trials. Subordinate birds took more worms than dominant birds on the SRI trials, $t(8) = 3.26, p < .05$, see Figure 9.

Subordinate vs. Dominant bird – Phase 1

The mean number of worms taken by dominant and subordinate birds during Phase 1 was compared for each trial type using an independent t-test for each comparison.

On the SRI training trials, dominant birds ate a similar number of worms as subordinate birds in Phase 1 of the SRI training trials, $t(8) = .49, ns$, see figure 10a. On the LRI training trials, dominant birds ate a similar number of worms as subordinate birds in Phase 1 of the LRI training trials, $t(8) = .50, ns$, see figure 10b. On the SRI control trials, dominant birds ate a similar number of worms as subordinate birds in Phase 1 of the SRI control trials, $t(8) = 1.00, ns$, See Figure 10c. Lastly, on the LRI probe trials, dominant birds ate a similar number of worms as subordinate birds in Phase 1 of the LRI probe trials, $t(8) = 1.37, ns$, see Figure 10d.

Latency to Enter Room

The latency of the subordinate bird to enter the room was compared across SRI training, LRI training, and LRI probe trials using a repeated measures analysis of variance.

Results indicate that subordinate birds entered the room at significantly different times on LRI probe trials, SRI training trials, and LRI training trials, $F(2,7) = 22.10, p < .01$, see Figure 11a.

Tukey's HSD indicated that subordinate birds took significantly longer to enter the room on LRI probe trials than on SRI training trials $q(3, 8) = 6.78, p < .01$, and LRI training trials, $q(3, 8) = 8.13, p < .01$.

Latency to Take a Worm

The latency of the subordinate bird to take a worm was compared across SRI training, LRI training, and LRI probe trials using a repeated measures analysis of variance.

Results indicate that subordinate birds took a worm at significantly different times on LRI probe trials, SRI training trials, and LRI training trials, $F(2,6) = 31.90, p < .01$, see Figure 11b.

Tukey's HSD indicated that subordinate birds took significantly longer to take a worm on LRI probe trials than on SRI training trials $q(3, 8) = 7.93, p < .01$, and LRI training trials, $q(3, 8) = 8.86, p < .01$.

Discussion

As in Experiment 1, it was hypothesized that birds would take more worms on the training trials on which they associated a retention interval with the dominant bird being absent, as compared to trials with retention intervals when the dominant bird was supposed to be

present. In Experiment 2, we found that subordinate birds took more worms on the SRI training trials when the dominant was absent as compared to the LRI training trials when the dominant bird was present and the LRI probe trials when the dominant bird was supposed to be present but was absent. These results suggest that birds were able to make an association that is contrary to naturalistic feeding situations in which it is more likely than a dominant bird will be finished eating after a short retention interval and will be gone after a long retention interval. These results provide yet more support for who-when memory in chickadees.

I also compared the number of worms taken by the subordinate bird on SRI training trials and dominant birds on SRI control trials as a control for passage of time. This measure was particularly important in Experiment 1 to control for birds' behavior after an LRI and was used as a control trial for birds' behavior after an SRI. In Experiment 2, subordinate birds took significantly more worms than dominant birds on SRI trials. These results can be interpreted as subordinates being more motivated to feed when they know they will be alone.

The number of worms taken in Phase 1 by subordinate and dominant birds was compared across all trial types to see whether the dominant birds were filling themselves up with worms during Phase 1, and therefore taking fewer worms than the subordinate bird during Phase 2. As indicated by the results, the subordinate birds were able to gain access to the meal worms during Phase 1 and took a similar number of worms across trial types. It is important to note that the birds were not food deprived prior to or during the experimental procedure which adds support to the suggestion that the subordinate birds took more worms than the dominant birds on the SRI control trials not as a function of hunger, but from having

learned the dominant bird would be absent and having access to the meal worms without interference by the dominant bird.

Subordinate chickadees were slower to enter the room from the start of the trial on LRI probe trials than SRI training trials or LRI training trials. Unlike in Experiment 1, subordinate birds were slower to enter the room when the dominant birds was learned be present but it was actually absent. They were significantly slower to enter the room on LRI probe trials than on LRI training trials when the dominant bird was actually present. It is possible that the birds were waiting for a cue to indicate the dominant bird had entered the room prior to entering the room themselves. It is not clear why this would be the case. In addition, dominant birds were not always visible on training trials because the perches and food platforms were not visible from all subordinate birds` home cages. Nevertheless, vocal cues from the dominant may have indicated that it was present on LRI training trials. Why subordinates should exhibit longer latencies to enter the room on LRI probe trials is not clear.

Subordinate birds were slower to take a worm on LRI probe trials than on SRI training or LRI training trials. They were slower to take a worm when the dominant bird was supposed to be present but it was actually absent than when the dominant bird was present or absent. Chickadee behavior is based on dominance hierarchies in their flock (Ekman 1989). In most Parid species, dominant birds have priority access to all available resources, including food (Ekman 1989). Dominant chickadees feed first and subordinate chickadees wait to have access to food, and can still be supplanted for their food after gaining access (Ficken et al, 1990). This feeding pattern can explain the subordinate bird taking longer to start feeding on an LRI probe trial when they learned the dominant birds would be present. If they are

anticipating the presence of a dominant bird, they may be waiting to see whether the dominant bird appears prior to starting to eat.

References

- Clayton, N. S., & Dickinson, A. (1998). What, where, and when: episodic-like memory during cache recovery by scrub jays. *Nature*, *395*, 272-274. doi: 10.1159/000096984
- Dally, J. M., Emery, N. J., & Clayton, N. S. (2006). Food-caching western scrub-jays keep track of who was watching when. *Science*, *312*, 1662-1665.
- Ekman, J. (1989). Ecology of non-breeding social systems of Parus. *Wilson Bulletin*, *101*, 263-288.
- Feeney, M.C., Roberts, W. A., & Sherry, D. F. (2009). Memory for what, where, and when in the black-capped chickadee (*Poecile atricapillus*). *Animal Cognition*, *12*, 767-777. doi:10.1007/s10071-009-0236-x
- Ficken M. S., Weise, C. M., & Popp, J. W. (1990). Dominance rank and resource access in winter flocks of black-capped chickadees. *Wilson Bulletin*, *102*(4), 623-633.
- Lundborg, K. and Brodin, A. (2003). The effect of dominance rank on fat deposition and food hoarding in the willow tit *Parus montanus* – an experimental test. *Ibis*, *145*, 78-82.
- Pravosudov, V. V. (2003). Long-term moderate elevation in corticosterone facilitates avian food caching behavior and enhances spatial memory. *Proceedings of the Royal Society B*, *270*, 2599-2604.
- Ratcliffe, L, Mennill, D. J., & Schubert, K. A. (2007). *Social Dominance and fitness in black-capped chickadees. Ecology and behavior of chickadees and titmice, an integrated approach. Oxford Ornithology.* (pp. 131 -139).

Smith, S. (1991). *The Black-capped Chickadee: Behavioral Ecology and Natural History*.
Cornell University Press, Ithaca.

Tulving, E. (1972). Episodic and semantic memory. In: Tulving: E, Donaldson W (eds),
Organization of memory. (pp. 381-398). Academic, San Diego.

Tulving, E. (1985). How many memory systems are there? *American Psychologist*, 40, 385-
398.

CHAPTER 3

General Discussion

Results from both Experiment 1 and Experiment 2 support the hypothesis that subordinate birds are able to remember who and when properties about social encounters. This conclusion is based on differential feeding patterns after short retention intervals (SRI) or long retention intervals (LRI) trials. In both experiments the subordinate birds took more worms after the retention interval that they associated with the dominant bird being absent and fewer worms on the retention interval trials when they learned the dominant bird would be present. This was even the case on the trials when the dominant bird was supposed to be present but was actually absent.

In Experiment 2, subordinate birds took more worms during Phase 2 of an SRI trial than Phase 2 of an LRI trial. These results provide important support for the results in Experiment 1. In Experiment 1, it was thought possible that subordinate birds took more worms after an LRI trial because they did not have access to worms for 1 hour versus 10 minutes in an SRI trial but the Experiment 2 results show that this was not the case. In Experiment 2, subordinate birds took more worms after an SRI than an LRI suggesting the number of worms taken is a function of the association between a retention interval and the dominant bird being absent or present versus a function of the passage of time.

In both experiments I controlled for interval length by comparing the mean number of worms taken by dominant and subordinate birds on LRI trials and SRI trials. This comparison was of particular importance in Experiment 1 to see whether the subordinate birds were taking more worms on the LRI training trials simply as a function of longer interval length rather than because they “knew” that the dominant bird would be absent. In both Experiment 1 and

Experiment 2, subordinate birds took more worms than the dominant birds took on the LRI and SRI trials, respectively. This could be explained by motivation of the subordinate bird. Perhaps when the subordinate birds had learned that they would be alone, they took advantage of this situation and ate more worms than normal.

As mentioned previously, subordinate birds tend to feed after the dominant bird has fed or is preoccupied with handling its own food (Ekman 1989). This explains the results of Phase 1 feeding in both Experiment 1 and Experiment 2. The mean number of worms taken was compared across subordinate and dominant chickadees for Phase 1 in all trial types. It was found that subordinate and dominant chickadees took a similar number of worms across trial types. In order to interpret our results, it is important to note that subordinate chickadees still had access to worms in Phase 1, once the dominant bird had left the food bowl or was preoccupied with eating a worm. This measure was useful in controlling for hunger of the subordinate birds versus dominant birds. Since both the dominant and subordinate bird had access to and consumed a similar number of worms, their hunger levels should have been similar in Phase 2 of the experiment, and thus differences in hunger could not account for why subordinate birds took more worms than dominant birds after an LRI trial (Experiment 1) or SRI trial (Experiment 2).

Unlike in Experiment 1 when subordinate birds entered the room at the same time across all trial types, in Experiment 2, subordinate birds were slower to enter the room on LRI probe trials when they learned the dominant bird would be present but it was actually absent. It is not clear why this would be the case and in particular, why this effect occurred in Experiment 2 but not Experiment 1.

An interesting question to ask is why subordinate birds acted as though a dominant bird was present on SRI probe trials (Experiment 1) and LRI probe trials (Experiment 2) when the dominant bird was visually absent. Even though an association was made between a specific retention interval and the dominant bird being present, it is interesting that the subordinate birds did not over-ride this association when they could visually see that the dominant bird was absent. The results from this study show comparable behavior on trials when the dominant bird was present (training trials) and absent (probe trials) suggesting that the subordinate birds did act as though the dominant bird was present instead of just freezing and not participating in the paradigm. These results suggest that a very strong association was made between a retention interval and the dominant bird being present or absent.

As with the experiment by Dally et al. (2006) examining who-memory in Western scrub-jays, this experiment provides support for a social component of memory in food-storing birds. Both species are capable of what-where-when memory as well as who memory. Western scrub-jays are food-storing birds that engage in tactics to minimize their food-caches from being pilfered (Dally et al. 2006). In the previous study, scrub-jays cached food in their home cages in the presence of either dominant, subordinate or partner birds, or with no observing bird. The number of re-caches made by the storing birds was elevated in the dominant and subordinate conditions, suggesting that they were aware of who was watching them cache food. Unlike in the experiment by Dally et al. (2006), the current study was able to provide a when component of episodic-like memory by manipulating retention intervals.

It is possible that the “who” component of our study may instead be a social “what”. Since birds were in the same dominance pair the entire experiment, subordinate birds were not required to recognize specific individuals. If subordinate birds had to distinguish between

specific individuals our results could more readily support the conclusion that black-capped chickadees have a who component of episodic-like memory instead of social “what” memory for the presence or absence of a dominant bird.

Humans provide evidence of episodic memory by responding to verbal questions asked by an examiner but this approach cannot be employed in animal research. Subordinate birds learned to associate specific retention intervals with the dominant bird being present or absent. Based on the number of worms taken, I inferred subordinate birds were able to learn when a dominant bird would be absent or present.

Zentall et al. (2001) state that in order for a memory to qualify as episodic memory, the test must be unexpected. If the test is expected, it is possible that semantic memory accounted for the response. For example, if you ask an individual what color shirt he wore yesterday, he will have to retrieve yesterday’s episode of getting dressed and recall what color shirt he wore. If you ask the individual the same question every day, he will learn to expect the question and prepare an answer ahead of time using semantic memory instead of episodic memory (Zentall et al. 2001). The current study used probe trials to test what the birds had learned. These probe trials were intermittently placed into the randomized training schedule to test the individual unexpectedly. By randomly testing the individual with probe trials, the experiment provided necessary evidence to support episodic-like memory in chickadees.

Based on these rules for distinguishing between semantic and episodic memory in animals, the current study adheres to the guidelines and provided support for the presence of episodic-like memory in black-capped chickadees.

The current experiment gives evidence for who and when memory in black-capped chickadees. In both of our experiments, regardless of whether the associations were

ecologically relevant, or presented in a backwards fashion, the subordinate birds were able to form strong associations between a retention interval and the dominant bird being absent or present.

Episodic memory is the ability to acquire and retain knowledge of events that were personally experienced as well as knowledge about their temporal order in subjective time and the capability to time travel mentally (Tulving 1985). Mental time travel is the ability to recollect past events or to anticipate future events that depend on episodic memory (Suddendorf and Corballis 2007). In the current study, birds had to recollect how long ago they encountered a dominant bird and then use the amount of time elapsed to predict what they would encounter in the next phase of the experiment. The results show that black-capped chickadees are capable of recollecting their last prior experience with a dominant bird and anticipate the presence or absence of that dominant bird. The use of mental time travel supports the presence of episodic-like memory in chickadees. Mental time travel in black-capped chickadees was previously examined by Feeney et al. (2011) who showed that chickadees were able to cognitively travel in time both retrospectively and prospectively using episodic memory.

In the current study, birds had to make use of internal interval timing to accurately predict whether a dominant bird would be present or absent in the next phase of the experiment. In Experiment 1, if a short interval had elapsed the dominant bird was still be present but was absent if a long interval has elapsed. The reverse was true in Experiment 2. The episodic-like component of this experiment required the birds to remember that they experienced a social encounter either a short or long time ago. Further experiments could use the peak procedure to examine the role of interval timing by birds in this experiment. In such an

experiment, the subordinate bird could be left alone in the observation room and its tendency to take worms observed as the SRI or LRI approached, occurred, and then passed. Interval timing would predict a peak in the suppression of worm consumption centered on the SRI or the LRI.

An interesting question is whether the results acquired from these experiments can be explained by Pavlovian conditioning. Is it possible that time intervals were a conditioned stimulus? A Pavlovian account might be that the dominant bird acts as an unconditioned stimulus and produces an unconditioned response such as fear in the subordinate bird. Fear, or a similar unconditioned response, would reduce the number of worms taken by the subordinate bird when the dominant bird was present. Repeated pairings of a time interval, either the SRI or the LRI, with the presence of the dominant bird would cause the time interval to become a conditioned stimulus and eventually occurrence of the time interval alone would produce a conditioned response such as fear and a reduction of the worms taken. A test of this idea might be an experiment to determine if time intervals can indeed act as conditioned stimuli in this way. A Pavlovian account would also suppose that since probe trials presented the conditioned stimulus alone without the dominant bird being present, the observed tendency to take worms in Experiment 1 and 2 was higher than if no probe trials had occurred. This is because the probe trials are essentially extinction trials with the conditioned stimulus of the time interval presented alone. This ought to reduce the association between the time interval and the unconditioned stimulus of “dominant bird present”. This too could be tested by experiment.

Based on the results from both Experiment 1 and 2, I can conclude that black-capped chickadees are capable of remembering who in conjunction with when. These components

of episodic-like memory could be useful in highly social, group-living species such as the black-capped chickadee. Black-capped chickadees form social flocks with linear dominance hierarchies that are stable over time and these dominance relations govern the behavior of subordinate birds (Smith 1991). For example, dominant birds have priority access to all available resources, including food (Ekman 1989). It would be reasonable to assume that chickadees would require who and when memory about the individuals and foods that they encounter.

The presence of episodic memory in non-human animals is a matter of debate and has recently become extensively studied. Episodic-like memory has been demonstrated in many species and the paradigms used, continue to evolve and provide new information on this ability in animals.

References

- Dally, J. M., Emery, N. J., & Clayton, N. S. (2006). Food-caching western scrub-jays keep track of who was watching when. *Science*, *312*, 1662-1665.
- Ekman, J. (1989). *Ecology of non-breeding social systems of Parus*. *Wilson Bulletin*, *101*, 263-288.
- Feeney, M.C., Roberts, W. A., & Sherry, D. F. (2011). Black-capped chickadees (*Poecile atricapillus*) anticipate future outcomes of foraging choices. *Journal of Experimental Psychology Animal Behavior Processes*, *37*(1), 30-40.
- Smith, S. (1991). *The Black-capped Chickadee: Behavioral Ecology and Natural History*. Cornell University Press, Ithaca.
- Suddendorf, T., & Corballis, M. C. (2007). The evolution of foresight: What is mental time travel and is it unique to humans? *Behavioral Brain Sciences*, *30*, 299-313.
- Tulving, E. (1985). How many memory systems are there? *American Psychologist*, *40*, 385-398.
- Zentall, T. R., Clement, T. S., Bhatt, R. S., & Allen, J. (2001). Episodic-like memory in pigeons. *Psychonomic Bulletin & Review*, *8*(4), 685-690.



Figure 1. The testing room setup in Experiment 1 and Experiment 2 for social training and testing. Birds' home cages were behind the automatic doors located on the testing room wall. Two perches and two food platforms were placed in the testing room. Birds were observed through a one-way mirror from the observation room.

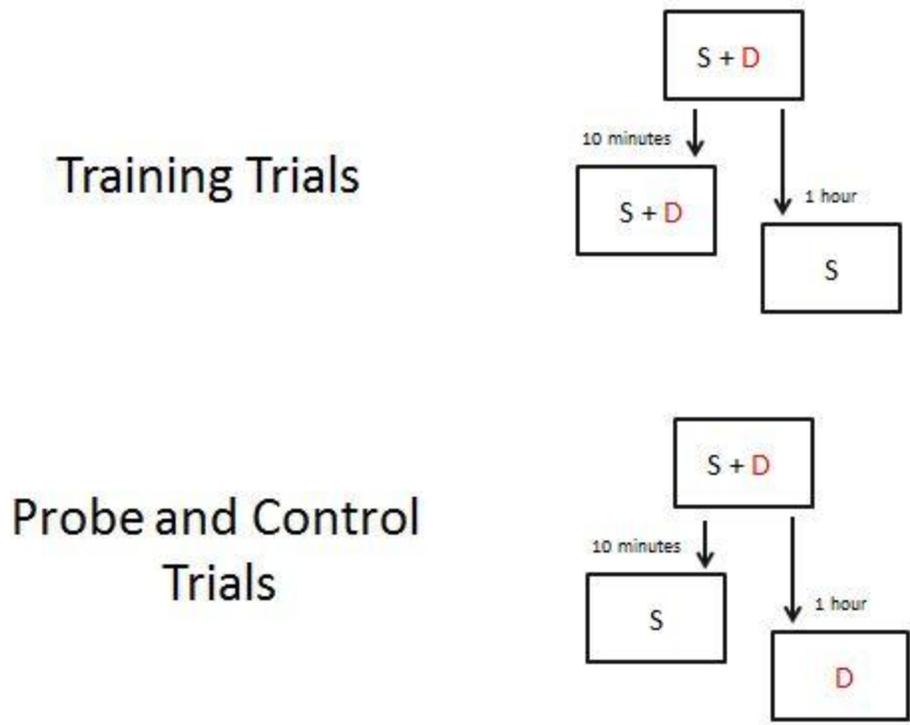


Figure 2. Training trials, probe trials and control trials followed the same basic procedure but switched the retention interval at which the dominant bird appeared. SRI training and probe trials commenced 10 minutes after the end of Phase 1, and LRI training and control trials commenced 1 hour after the end of Phase 1. See text for details.

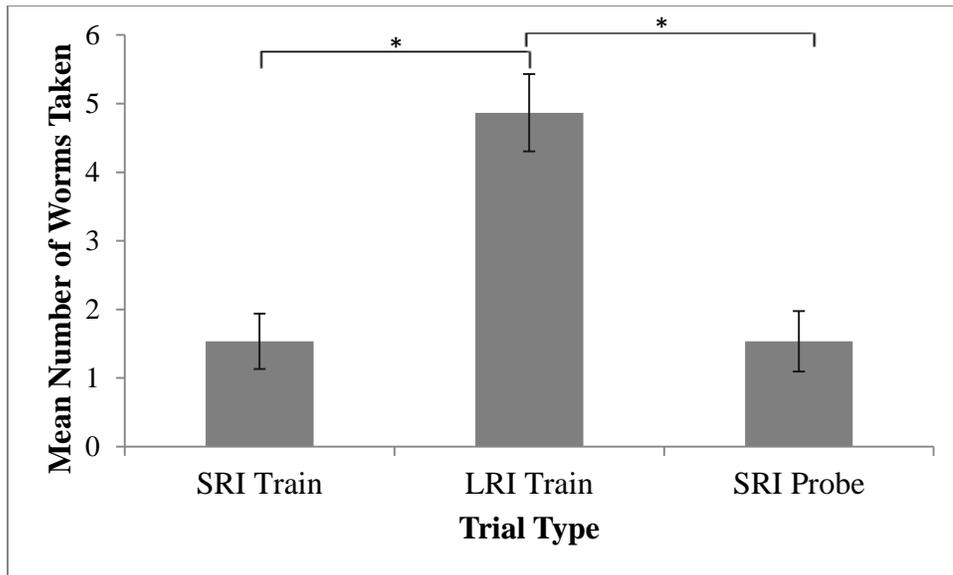


Figure 3. Experiment 1. Mean number of worms taken by subordinate birds on SRI training, LRI training, and SRI probe trials. All error bars = ± 1 SEM.

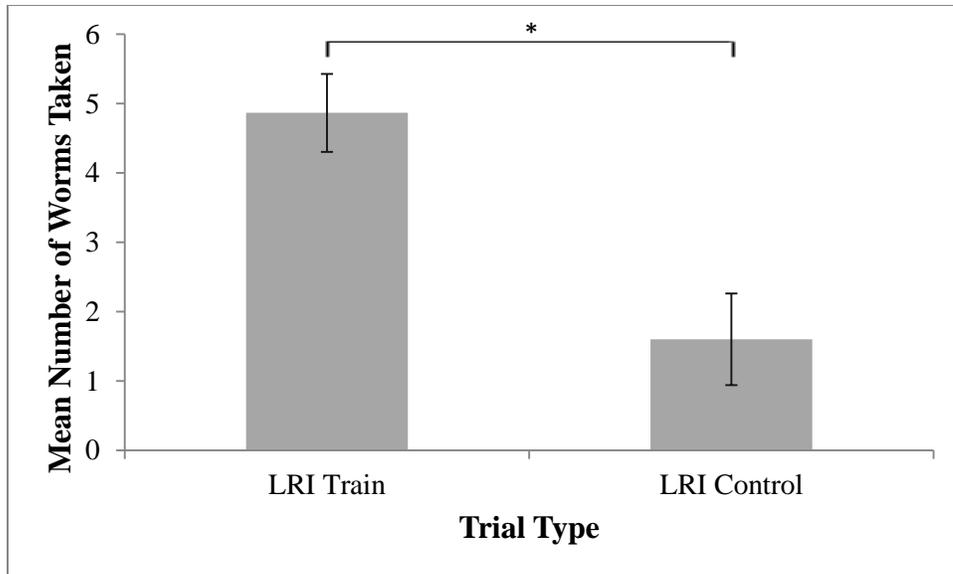


Figure 4. Experiment 1. Mean number of worms taken by dominant birds on LRI control trials and subordinate birds on LRI training trials. All error bars = ± 1 SEM.

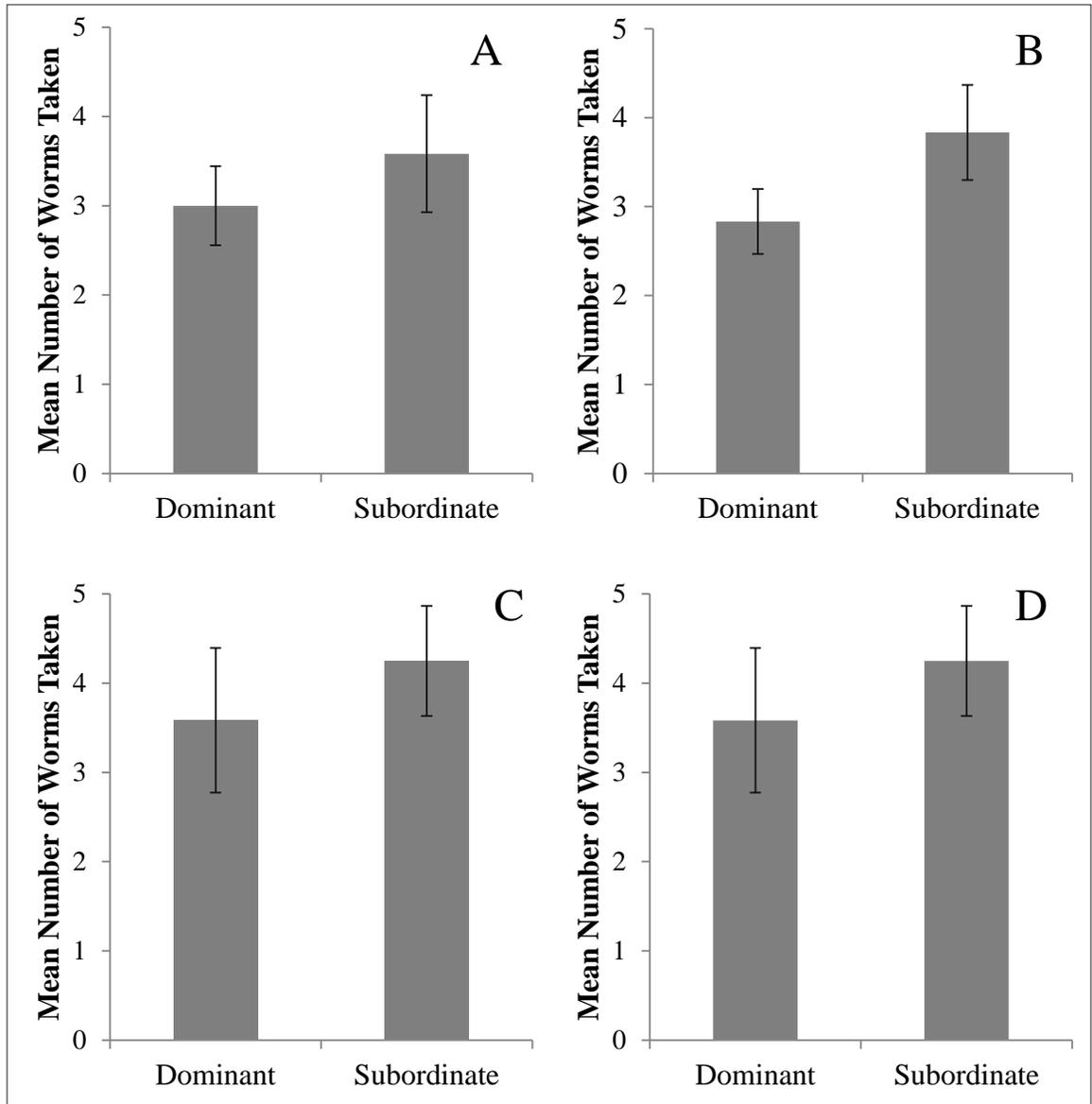


Figure 5. Experiment 1. Mean number of worms taken by subordinate and dominant birds during Phase 1 of SRI training trials (A), LRI training trials (B), SRI probe trials (C), and LRI control trials (D). All error bars = ± 1 SEM.

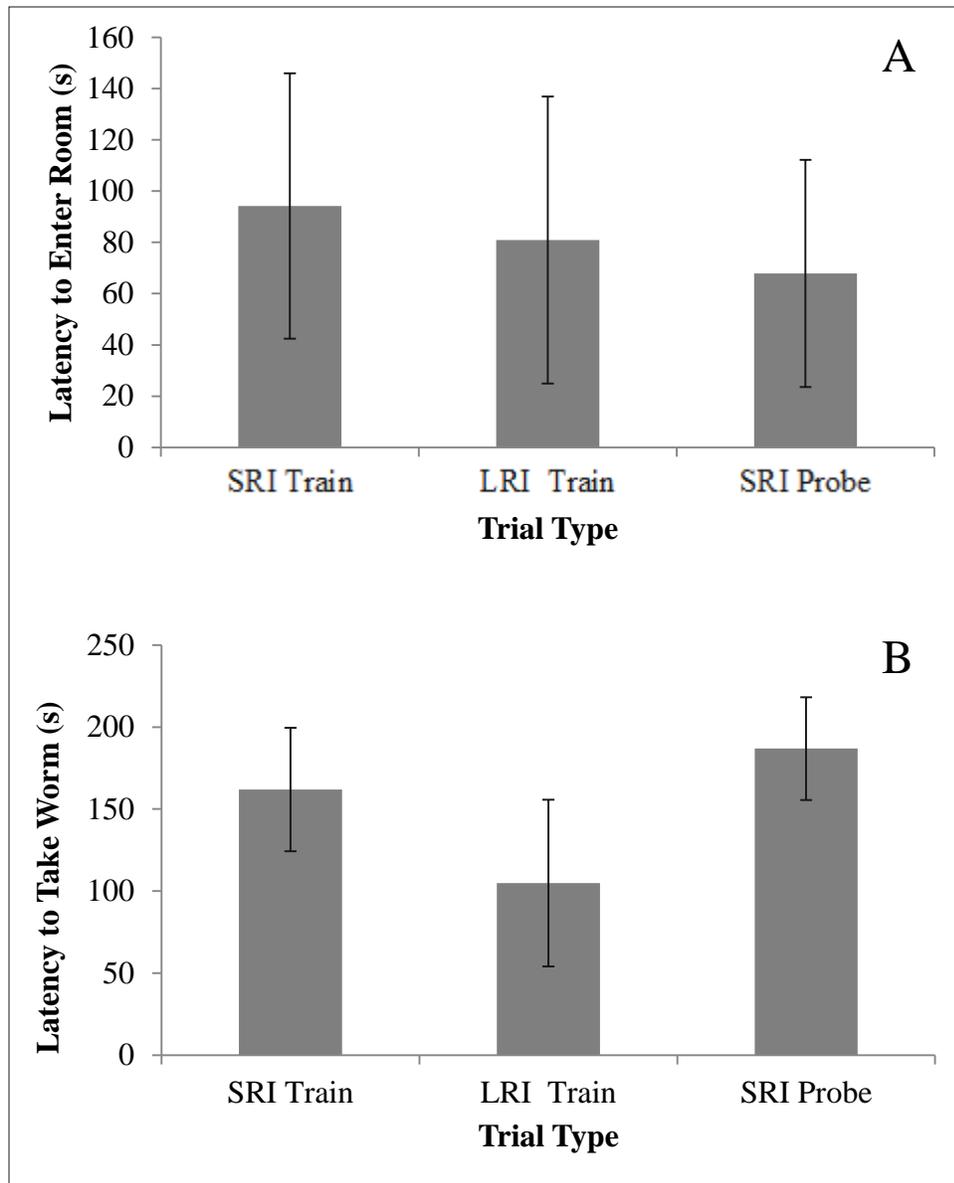
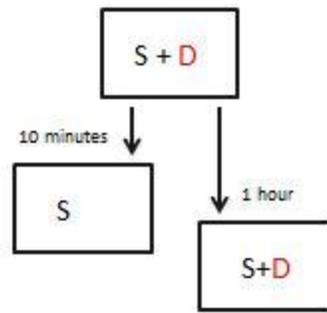


Figure 6. Experiment 1. Latency to enter the testing room by the subordinate birds from start of trial (A). Latency to take a worm by the subordinate birds at the start of each trial type (B). All error bars = \pm 1SEM.

Training Trials



Probe and Control Trials

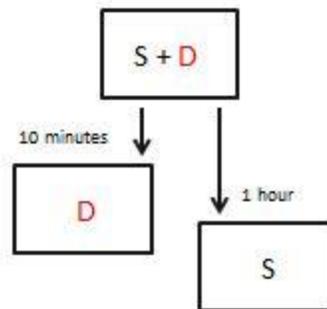


Figure 7. Training trials, probe trials and control trials followed the same basic procedure but switched the retention interval at which the dominant bird appeared. SRI training and control trials commenced 10 minutes after the end of Phase 1 and LRI training and probe trials commenced 1 hour after the end of Phase 1. See text for details.

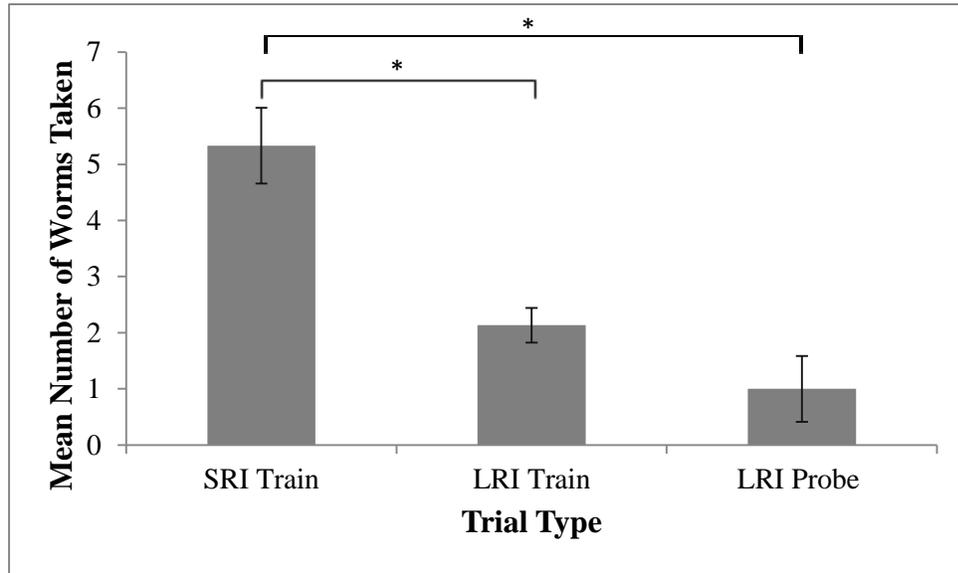


Figure 8. Experiment 2. Mean number of worms taken by subordinate birds on SRI training, LRI training, and LRI probe trials. All error bars = ± 1 SEM.



Figure 9. Experiment 2. Mean number of worms taken by subordinate birds on SRI training trials and dominant birds on SRI control trials. All error bars = ± 1 SEM.

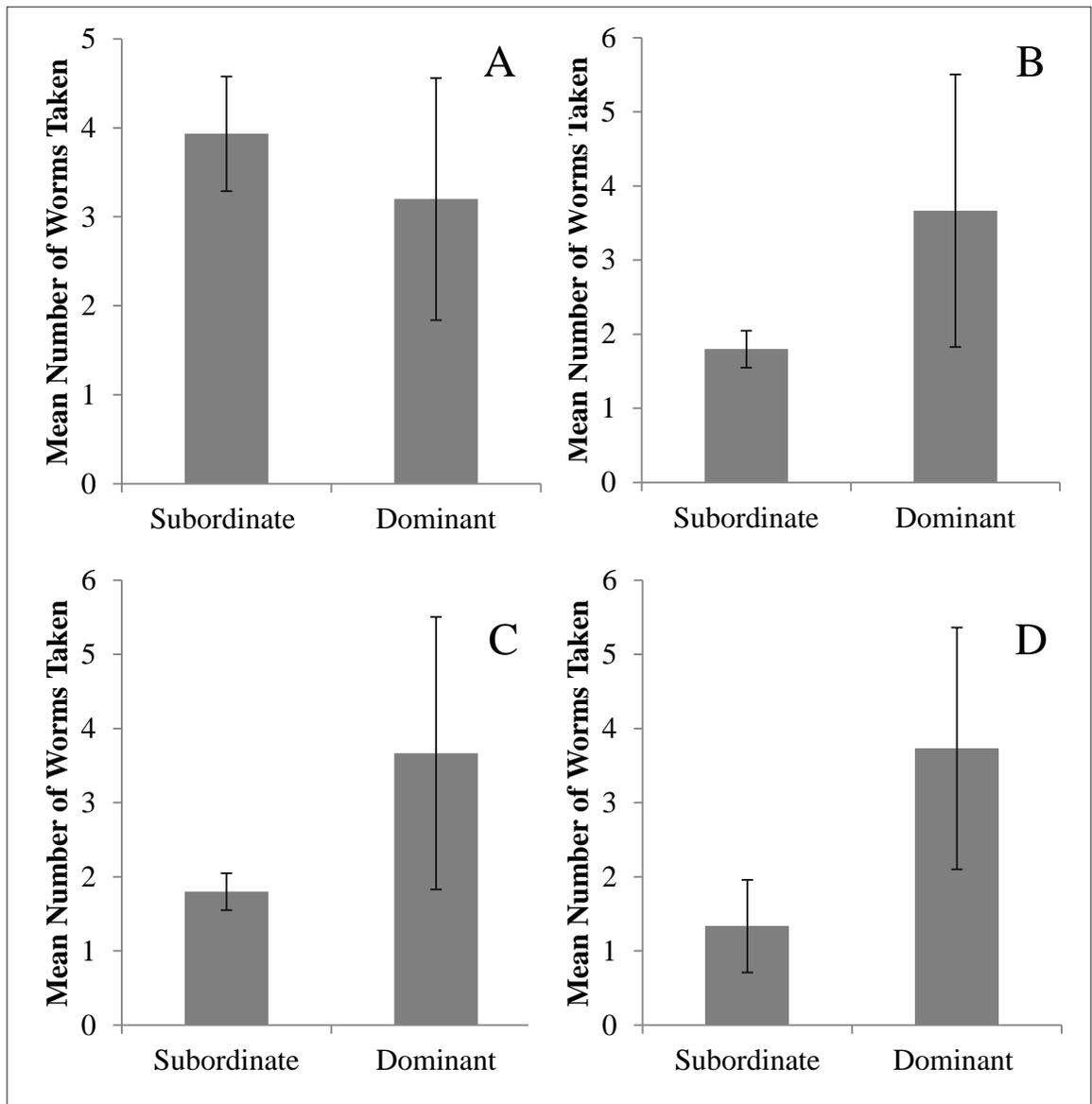


Figure 10. Experiment 2. Mean number of worms taken by subordinate and dominant birds during Phase 1 of SRI training trials (A), LRI training trials (B), SRI control trials (C), and LRI probe trials (D). All error bars = ± 1 SEM.

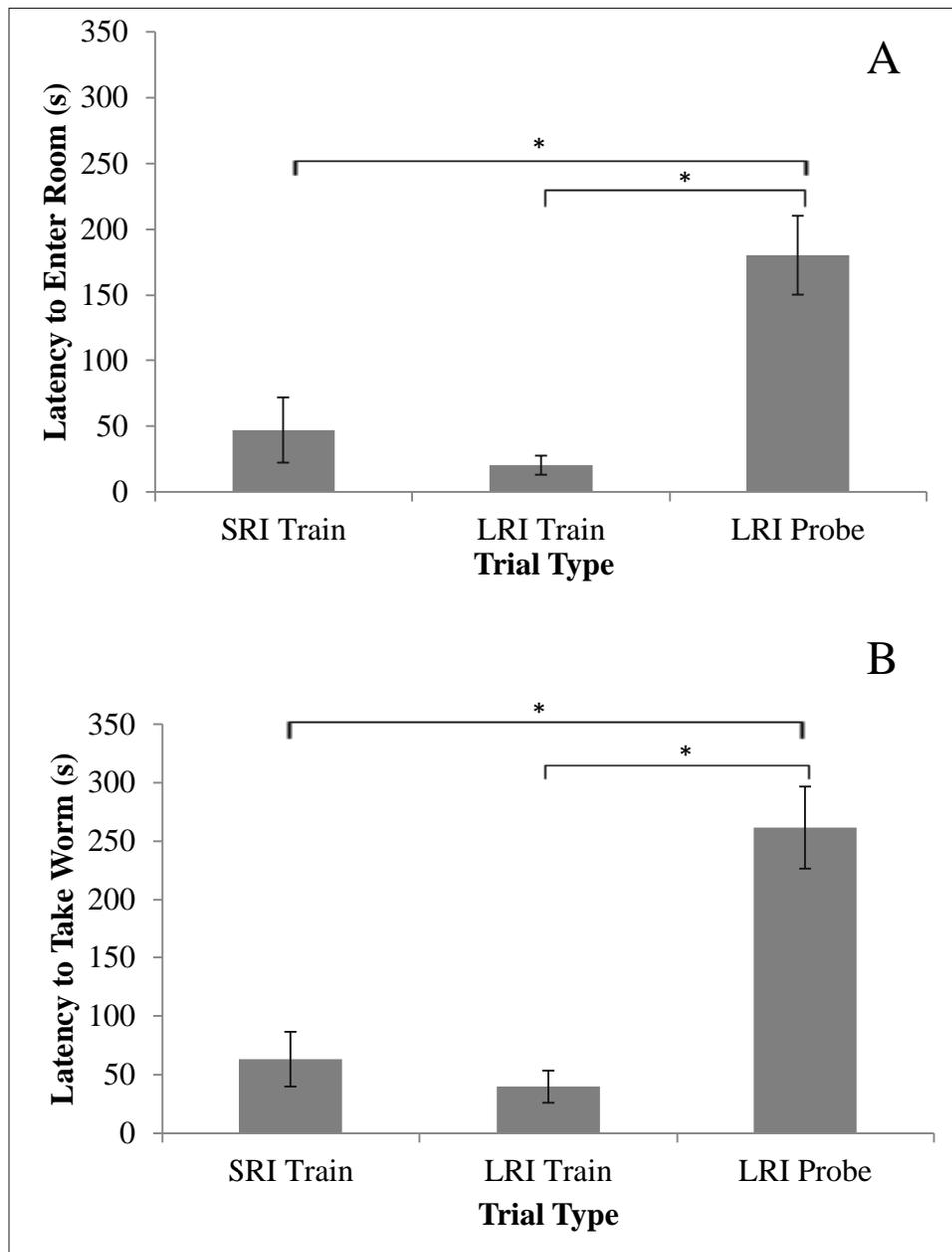


Figure 11. Experiment 2. Latency to enter the testing room by the subordinate birds from start of trial (A). Latency to take a worm by the subordinate birds at the start of each trial type (B). All error bars = ± 1 SEM.



Environment Environnement
Canada Canada

CANADIAN WILDLIFE SERVICE - PERMIT PERMIS - SERVICE CANADIEN DE LA FAUNE

		Permit to for Permis de/pour	Permit no. No de permis
		SCIENTIFIC	CA 0236
Organization Organisation	University of Western Ontario	Issued under section Délivré en vertu de l'article	of de
		19	MIGRATORY BIRD REGULATIONS
Surname Nom de famille	Sherry	Name Prénom	Department Département
		Dr. David	Dept. of Psychology

Date of issue Date d'émission	Date of expiry Date d'expiration
April 26, 2011	December 31, 2011
Signature of holder Signature du détenteur	For the minister Pour le ministre

Special Conditions - Conditions spéciales

1. Prior to any use of this permit local game authorities (OMNR) are to be notified relative to collecting procedures, times and localities of collection.
2. Landowner's permission must be obtained prior to collecting on private property.
3. Permit or a copy of the permit to be carried in the field by all collectors.
4. The permit holder is authorized, for scientific research purposes, to live capture and to hold in captivity a maximum of 50 adult Black-capped Chickadee (*Parus atricapillus*), 50 adult White-breasted Nuthatch (*Sitta carolinensis*) and 50 adult Dark-eyed Junco (*Junco hyemalis*) from sites as located in Southwestern Ontario.
5. A maximum of 25 of each species may be sacrificed for further analysis.
6. Specimens to be transferred to the University of Western Ontario (London) for further study.
7. Any specimens not retained for study purposes to be disposed of by burial or by approved laboratory waste disposal methods.
8. All specimens that are to be released must be done so at the site of their initial capture.
9. All collected birds to be humanely handled, sampled, and released according to Animal Care Committee protocol of the University of Western Ontario.
10. Nests or young birds in nests are not to be disturbed, damaged or destroyed.
11. Permit holder shall submit a written report, by 31 January 2012, indicating the results of the study to the Canadian Wildlife Service, 867 Lakeshore Road, Burlington, ON., L7R 4A6.
12. Nominees authorized to act under the direction of the permittee are: Seasonal assistants as acting under the immediate direction of the permit holder.

Environment Canada / Environnement Canada



Canada



AUP Number: 2007-001-03
PI Name: Sherry, David
AUP Title: Neurogenesis, Spatial Memory, And Animal Cognition

Official Notice of Animal Use Subcommittee (AUS) Approval: Your new Animal Use Protocol (AUP) entitled "Neurogenesis, Spatial Memory, And Animal Cognition

" has been APPROVED by the Animal Use Subcommittee of the University Council on Animal Care. This approval, although valid for four years, and is subject to annual Protocol Renewal.2007-001-03::5

1. This AUP number must be indicated when ordering animals for this project.
2. Animals for other projects may not be ordered under this AUP number.
3. Purchases of animals other than through this system must be cleared through the ACVS office. Health certificates will be required.

The holder of this Animal Use Protocol is responsible to ensure that all associated safety components (biosafety, radiation safety, general laboratory safety) comply with institutional safety standards and have received all necessary approvals. Please consult directly with your institutional safety officers.

Submitted by: Copeman, Laura
on behalf of the Animal Use Subcommittee
University Council on Animal Care

The University of Western Ontario
Animal Use Subcommittee / University Council on Animal Care
Health Sciences Centre, • London, Ontario • CANADA - N6A 5C1
PH: 519-661-2111 ext. 86768 • FL 519-661-2028
Email: auspc@uwo.ca • http://www.uwo.ca/animal_website/

CIRRICULUM VITAE

Alisha Ann Wiechers

Education:

MSc.	2010-2012	Western University Department of Neuroscience <i>Supervisor: Dr. D.F. Sherry</i>
HBSc.	2005-2010	Western University Department of Psychology <i>Supervisor: Dr. D.F. Sherry</i>

Interests

Keywords: animal cognition, what-where-when memory, social behavior, dominance, neurogenesis, seasonality, hippocampus, food-storing, black-capped chickadee

Awards and Scholarships:

2011-2012	Western Graduate Thesis Award
2011-2012	Ontario Graduate Scholarship (OGS)
2010-2012	Western Graduate Scholarship
2007-2012	Dean's Honour List
2005-2007	Daimler Chrysler Scholarship

Publications:

Manuscripts in Preparation

Wiechers, A. A., & Sherry, D.F. (2012). Episodic-like memory for who and when in the black-capped chickadee (*poecile atricapillus*).

Wiechers, A. A., & Sherry, D.F. (2012). • Endogenous markers of adult hippocampal neurogenesis in black-capped chickadees (*poecile atricapillus*).

Presentations:

Wiechers, A. A., & Sherry, D.F. (2011). Endogenous markers of adult hippocampal neurogenesis in black-capped chickadees (*poecile atricapillus*). Poster presented at the 41st Society for Neuroscience Conference, Washington, D.C.

Wiechers, A. A., Barrett, M.C., & Sherry, D.F. (2011). Who memory in the Black-capped Chickadee. Lecture at Western University Neuroscience Summer School, London, Ontario.

Wiechers, A. A., & Sherry, D.F. (2010). Endogenous markers of adult hippocampal neurogenesis in black-capped chickadees (*poecile atricapillus*). Poster presented at the Honours Thesis Conference at the Western University, London, Ontario.

Teaching Experience:

2010-2011

Teaching Assistant, Psych 1000, Introduction to Psychology, Department of Psychology, Western University.