Comparative studies of cognitive abilities in the Paridae

Evidence from laboratory studies

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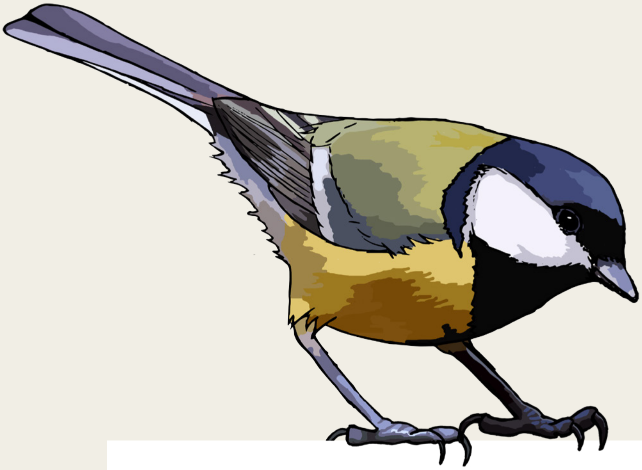

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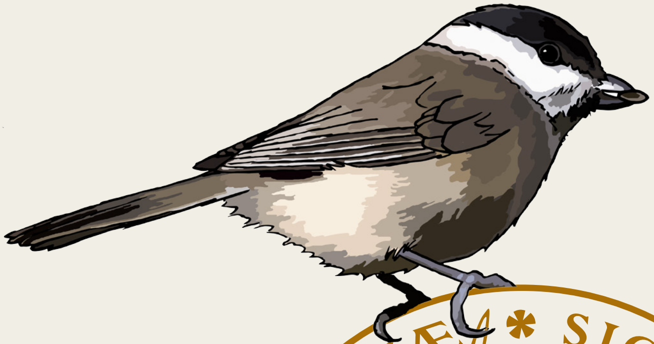

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Utku Urhan

LUND
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Title and subtitle: Comparative studies of cognitive abilities in the *Paridae* – evidence from laboratory studies

Abstract - The *Paridae* (tits, titmice and chickadees) is a bird family consisting of both food hoarding and non-hoarding species. Many studies have been conducted on birds that are considered to be cognitively advanced, such as parrots and corvids, whereas much less is known about these small passerines. In this thesis, I have investigated the cognitive abilities of two members of the *Paridae* family; marsh tits and great tits. There is a clear dichotomy in wintering strategy across *Paridae*, with these two species representing either side. Marsh tits are scatter hoarders that cryptically cache food over large areas, whereas great tits are a non-hoarding generalist species that are known to be particularly behaviourally innovative. First, I tested the spatial memory of marsh tits in a laboratory specifically designed for food hoarding studies. In nature, spatial memory is essential for scatter food hoarders to retrieve cached food. Marsh tits displayed around 40% retrieval success after 10 retrieval attempts. These results were in accordance with the previous food hoarding studies conducted on captive marsh tits. I also tested humans in the same task and found they performed much better than marsh tits as after just five attempts they retrieved 80% of the hidden food. Since marsh tits have specialised spatial memory, one may have expected them to outperform humans. The fact that this was not the case, led us to consider whether the marsh tits were affected by proactive memory interference, whereby more recent memories deteriorate as a result of repeated testing. However, this was not the case, as marsh tits performed similarly in all repetitions of the test. Next, I turned my focus to great tits. It is likely to be advantageous for great tits to have access to food caches created by food hoarders during cold winter months. I investigated whether great tits are capable of memorising the locations of caches created by marsh tits. Great tits were allowed to observe marsh tits while they were hiding food items. They successfully memorised the location of caches made by marsh tits after one hour and 24 hours retention intervals. Although it is remarkable that great tits can memorise caches made by marsh tits, we do not know if this ability is found in other *Paridae* species. In paper IV, I therefore tested the observational spatial memorisation ability of marsh tits in the same experimental setup. Marsh tits were unable to retrieve the caches they observed being stored by other marsh tits. This implies that they do not use this strategy for foraging and that this ability is not common to all *Paridae* species.In the *Paridae* family, sex differences are most pronounced in great tits with clear differences in behaviour, morphology and social hierarchy. Hence, I investigated sex differences in cognition in great tits. In chapter V, I investigated whether males and females displayed differences in cognitive abilities using the observational spatial memory task. Female great tits out performed males in this task. In paper VI, I tested for sex differences in the motor self-regulation ability of great tits using the transparent cylinder task. In this task, a food reward is placed inside a transparent cylinder with openings at both ends. The animal must therefore inhibit its urge to reach directly for the visible food and instead take a detour to one of the open end of the cylinder. In addition, I separated the birds into two groups; one with experience of the cylinder and another with no prior experience. Cylinder-experienced birds had a similar transparent cylinder in their cage for three days prior to the experiment whereas cylinder-naïve birds first encountered the transparent cylinder during the test. Great tits were generally successful at this task. I found no overall sex difference in motor self-regulation ability, however the number of repeats that was required to master the task differed between females and males. Males quickly mastered the task, even with no prior experience. However, males with prior experience did not outperform naïve males. Although females took longer to learn the task, those with prior experience outperformed naïve females. In conclusion, I found cognitive differences between two species that differ in their foraging strategies within the same taxonomic family. I propose that these differences have developed due to the distinct winter foraging strategies of these species. I also found evidence of cognitive sex differences in great tits, which I suggest are the result of sex differences in social hierarchy.

Key words: comparative cognition, spatial memory, food hoarding, observational spatial memory, motor self-regulation, cognitive sex differences, foraging strategy

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It is just like man's vanity and impertinence to call an animal dumb because it is dumb to his dull perceptions.

Mark Twain

Content

List of Papers

I. Brodin, A., & Urhan, A. U. (2013). An evaluation of memory accuracy in food hoarding marsh tits *Poecile palustris* - how accurate are they compared to humans? Behavioural Processes, 97, 25–32.

II. Brodin, A., & Urhan, A. U. (2014). Interspecific observational memory in a non-caching Parus species, the great tit *Parus major*. Behavioral Ecology and Sociobiology, 68(4), 649–656.

III. Brodin, A., & Urhan, A. U. (2015). Sex differences in learning ability in a common songbird, the great tit — females are better observational learners than males. Behavioral Ecology and Sociobiology, 69(2), 237–241.

IV. Urhan, A. U., & Brodin, A. (2015). No evidence for memory interference across sessions in food hoarding marsh tits *Poecile palustris* under laboratory conditions. Animal Cognition, 18(3), 649–656.

V. Urhan, A. U., Emilsson, E., & Brodin, A. (2017). Evidence against observational spatial memory for cache locations of conspecifics in marsh tits *Poecile palustris*. Behavioral Ecology and Sociobiology, 71(2), 34.

VI. Urhan, A. U., Isaksson, E., & Brodin., A. (2017) Sex difference in learning rate of motor self-regulation in great tits, *Parus major* (Manuscript)

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Author contributions

I. AUU and AB conceived and designed the study, AB captured the birds, AUU trained the birds and performed the experiments, AUU and AB analysed the data, AB drafted the manuscript. AUU and AB contributed to the final manuscript.

II. AUU and AB conceived and designed the study, AB captured the birds, AUU trained the birds and performed the experiments, AUU and AB analysed the data, AB drafted the manuscript, AUU and AB contributed to the final manuscript.

III. AUU and AB conceived and designed the study, AB captured the birds, AUU trained the birds and performed the experiments, AUU and AB analysed the data, AB and AUU drafted the manuscript. AUU and AB finalised the manuscript.

IV. AUU and AB conceived and designed the study, AB captured the birds, AUU trained the birds and performed the experiments, AUU and AB analysed the data, AUU drafted the manuscript. AUU and AB contributed to the final manuscript.

V. AUU and AB conceived and designed the study, AB captured the birds, AUU and EE trained the birds and performed the experiments, AUU and AB analysed the data, AUU drafted the manuscript. All authors contributed to the final manuscript.

VI. AUU and AB conceived the study. AUU , AB and EI designed the study. AB captured the birds. AUU and EI trained the birds and performed the experiments. AUU drafted the manuscript and analysed the data. All authors contributed to the final manuscript.

Authors

Anders Brodin (AB), AUU (Utku Urhan), Ellen Emilsson (EE), Emil Isaksson (EI)

Abstract

The *Paridae* (tits, titmice and chickadees) is a bird family consisting of both food hoarding and non-hoarding species. Many studies have been conducted on birds that are considered to be cognitively advanced, such as parrots and corvids, whereas much less is known about these small passerines. In this thesis, I have investigated the cognitive abilities of two members of the *Paridae* family; marsh tits and great tits. There is a clear dichotomy in wintering strategy across *Paridae*, with these two species representing either side. Marsh tits are scatter hoarders that cryptically cache food over large areas, whereas great tits are a non-hoarding generalist species that are known to be particularly behaviourally innovative.

First, I tested the spatial memory of marsh tits in a laboratory specifically designed for food hoarding studies. In nature, spatial memory is essential for scatter food hoarders to retrieve cached food. Marsh tits displayed around 40% retrieval success after 10 retrieval attempts. These results were in accordance with the previous food hoarding studies conducted on captive marsh tits. I also tested humans in the same task and found they performed much better than marsh tits as after just five attempts they retrieved 80% of the hidden food. Since marsh tits have specialised spatial memory, one may have expected them to outperform humans. The fact that this was not the case, led us to consider whether the marsh tits were affected by proactive memory interference, whereby more recent memories deteriorate as a result of repeated testing. However, this was not the case, as marsh tits performed similarly in all repetitions of the test.

Next, I turned my focus to great tits. It is likely to be advantageous for great tits to have access to food caches created by food hoarders during cold winter months. I investigated whether great tits are capable of memorising the locations of caches created by marsh tits. Great tits were allowed to observe marsh tits while they were hiding food items. They successfully memorised the location of caches made by marsh tits after one hour and 24 hours retention intervals.

Although it is remarkable that great tits can memorise caches made by marsh tits, we do not know if this ability is found in other *Paridae* species. In paper IV, I therefore tested the observational spatial memorisation ability of marsh tits in the same experimental setup. Marsh tits were unable to retrieve the caches they observed being stored by other marsh tits. This implies that they do not use this strategy for foraging and that this ability is not common to all *Paridae* species.

In the *Paridae* family, sex differences are most pronounced in great tits with clear differences in behaviour, morphology and social hierarchy. Hence, I investigated sex differences in cognition in great tits. In chapter V, I investigated whether males and females displayed differences in cognitive abilities using the observational

spatial memory task. Female great tits out performed males in this task. In paper VI, I tested for sex differences in the motor self-regulation ability of great tits using the transparent cylinder task. In this task, a food reward is placed inside a transparent cylinder with openings at both ends. The animal must therefore inhibit its urge to reach directly for the visible food and instead take a detour to one of the open end of the cylinder. In addition, I separated the birds into two groups; one with experience of the cylinder and another with no prior experience. Cylinder-experienced birds had a similar transparent cylinder in their cage for three days prior to the experiment whereas cylinder-naïve birds first encountered the transparent cylinder during the test. Great tits were generally successful at this task. I found no overall sex difference in motor self-regulation ability, however the number of repeats that was required to master the task differed between females and males. Males quickly mastered the task, even with no prior experience. However, males with prior experience did not outperform naïve males. Although females took longer to learn the task, those with prior experience outperformed naïve females.

In conclusion, I found cognitive differences between two species that differ in their foraging strategies within the same taxonomic family. I propose that these differences have developed due to the distinct winter foraging strategies of these species. I also found evidence of cognitive sex differences in great tits, which I suggest are the result of sex differences in social hierarchy.

Popular summary

Every animal has a repertoire of behaviours that are fixed and "hard-wired" in to the brain. These behaviours have frequently evolved due to regular changes in nature, such as day and night, seasons etc. However, many factors are of course unpredictable in nature. In order to cope with such unpredictable changes, animals must have some flexibility in their behaviour. Cognition is a process that makes it possible to have such behavioural flexibility, as it helps the animal to obtain information from its surroundings, to save this information, and later use it in order to modify its behaviour according to environmental changes.

Cognition has evolved separately in many groups of animals and due to this and various selection pressures, cognitive ability varies considerably among animals. Because of these differences, comparative cognition studies have become very important, as it allows us to investigate cognitive variation between species, and even variation in the sexes within the same species.

In my thesis, I have investigated two species in a songbird family, the *Paridae* (tits, chickadees, titmice). The members of this family that are living in Sweden, and Northern Europe, have two distinct winter foraging strategies; they are either large-scale food hoarders or generalist foragers that do not store food. Most food hoarding birds are scatter hoarders, meaning that they hide many food items in separate locations over a large area. Most parids are food hoarders and they rely on a specialized spatial memory to relocate their caches. There are, as mentioned above, also non-hoarding parids that are generalist foragers, which means that they are more diverse when it comes to food sources.

In order to investigate cognitive differences in these two groups, I tested one member from each, under laboratory conditions in the animal facility in Lund University, Sweden. I tested marsh tits *Poecile palustris*, food hoarding specialists, and great tits *Parus major*, non-hoarding generalists. Marsh tits are able to cache and retrieve thousands of seeds in a year. Great tits on the other hand can exploit many different types of food sources by foraging techniques that can be considered innovative.

In paper I, I tested the spatial memory of marsh tits in an indoor arena specifically designed for food hoarding studies. Spatial memory is the type of memory that allow animals to memorise locations and it is an essential mechanism for scatter food hoarders to retrieve cached food. I allowed marsh tits to hide five seeds in a setup where there are 100 possible caching locations. Then, either five or 24 hours later I allowed them to retrieve these caches. Marsh tits had around 40% retrieval success in the first 10 retrieval attempts. These results were in accordance with previous similar food hoarding studies of marsh tits and related species. I also tested humans in the same task. Humans were much better than the birds and retrieved 80% of the hidden food in the first five attempts.

Since marsh tits are known to possess a highly specialised caching memory, one may assume that they should outperform humans, especially in a task that is seemingly irrelevant to humans. This led me to think that the performance of the marsh tits may be affected by so called proactive memory interference. This is an effect that causes deterioration of more recent memories due to previous ones. In our experiments the birds have been storing and searching repeatedly in the same caching holes due to repeated testing. In nature they always store in new sites. To test for such memory interference I allowed marsh tits to cache and retrieve five seeds in the same setup in three repeated sessions (paper II). However, I found no evidence for any memory interference as the marsh tits performed similarly in all three session of the test.

I then, in paper III, turned my focus to great tits. I investigated whether great tits are capable of observing and memorizing locations of caches that are made by marsh tits. In winter, when the food is scarce, this ability can help great tits to access food that has been cached by food hoarders .In order to test this idea, I allowed caged great tits to observe hoarding marsh tits in the same setup where I previously had tested the marsh tits' retrieval accuracy. The great tits were capable of memorizing the location of caches that were made by marsh tits. Such observational memorisation is presumably more difficult than memorisation of own caches.

Although it is quite remarkable that great tits can memorise caches made by marsh tits, we do not know whether this ability is a common foraging skill in parids. In paper IV therefore I tested marsh tits in the same observational spatial memorisation test in which I previously had tested great tits. Marsh tits were not able to retrieve the caches that they observed being stored by other marsh tits. This implies that they do not have this skill and that it is not a common ability in parids.

In parids, sex differences are most clearly pronounced in the great tit, with clear differences in behaviour, plumage colouration and dominance rank. Hence, I think it is logic to search for possible sex differences in cognition in great tits. In paper V, I investigated if there were any sex differences in the same observational memory task as in paper III, memorisation of marsh tit caching location. The rationale was that there appeared to be such differences already in paper III, but as half of the sessions had been made in spring, the poor performance of the males may have depended on them being in a breeding condition. Interestingly, female great tits were much better at this task also when males were not in a breeding condition. As males are dominant over females, they will have prior access to food in nature. It will then benefit a subordinate female to be able to return to a marsh tit cache later, when no bullying males are around.

In paper VI, I continued my search for cognitive sex differences in motor-self regulation ability. Motor self-regulation, is an ability essential for higher forms of self-control. To do this I tested great tits in the transparent cylinder task. In this task, animals have to control their urge to go directly for a visible reward (a preferred food item) that is inside a perpendicularly positioned transparent cylinder. If they can refrain from the instant urge to peck at the cylinder wall and instead make a detour to an open end of the cylinder and retrieve the reward this way, they pass the test. In addition, I assigned the birds to two treatment groups; those that had previous experienced of the cylinder and those that were naïve to it. Cylinder-experienced birds had an empty transparent cylinder at the bottom of their cage for three days prior to the experiment, whereas cylinder-naïve birds saw the transparent cylinder for the first time during the test. Great tits were good at this task in general. I found no overall sex difference but the speed with which the task was learnt differed between the sexes. The males mastered this task rather fast despite not having prior experience with the cylinder, however they did not perform better if they were cylinder-experienced. Females, on the other hand performed better when they had prior experience with the transparent cylinder and outperformed other experienced males.

In conclusion, I found cognitive differences between two species of parids. I suggest that these differences have developed due to differences in winter foraging strategies in these species. I also found some evidence for cognitive sex differences in great tits, which I suggest are the result of differences in dominance rank between the sexes in this species.

Populärvetenskaplig sammanfattning

Många beteenden hos djur kan vara oflexibla och mer eller mindre ”hard-wired” i hjärnan. Sådana beteenden kan vara ändamålsenliga för regelbundna och rytmiska förändringar i naturen, såsom dag och natt, årstider, etc. Men många faktorer är naturligtvis oförutsägbara i naturen. För sådana oförutsägbara förändringar är det bättre för djur att vara flexibla i sitt beteende. Kognition är en process som gör det möjligt att ha sådan beteendemässig flexibilitet. Exempelvis kan kognitiv inlärning göra det möjligt för ett djur att förstå information från omgivningen, att spara denna information och använda den senare för att modifiera sitt beteende enligt denna.

Kognitiv förmåga har utvecklats separat i många grupper av djur och både p g av detta och skillnader i selektion från omgivningen, finns det stor kognitiv variation mellan olika djur. För att förstå hur kognition fungerar och har utvecklats har jämförande kognitionsstudier blivit mycket viktiga, eftersom vi kan undersöka skillnader mellan arter och till och med variation mellan könen inom samma art.

I denna avhandling har jag undersökt kognition hos två arter mesfåglar (*Paridae*). De arter i mesfamiljen som förekommer i Sverige, och Nordeuropa, har endera av två helt olika strategier för vinteröverlevnad. Antingen är de storskaliga födohamstrare som håller revir året om, eller också är de kringstrykande generalister som inte hamstrar. Hamstrande mesar är s.k. spridningshamstrare som gömmer frön och larver i tusentals separata gömställen utspridda i ett stort vinterrevir. Hamstrande mesar skyddar sina förråd genom att gömmena är kryptiska eller t.o.m. övertäckta. För att själva hitta tillbaka till sina gömmen är därför hamstrande mesar beroende av ett speciellt välutvecklat rumsligt minne. De flesta Europeiska mesarna är sådana spridningshamstrare, men det finns åtminstone två arter som tillhör den andra kategorin, kringstrykande generalister, talgoxen *Parus major*, och blåmesen, Cyanistes caeruleus. Eftersom dessa arter är Europas vanligaste mesar får man anta att de är mycket framgångsrika med denna strategi.

För att undersöka kognitiva skillnader mellan dessa två grupper har jag arbetat med en art från varje grupp i inomhusförsök i djuranläggningen på biologiska institutionen vid Lunds universitet. Jag har gjort olika försök på entitor *Poecile palustris*, en hamstrande art som är vanlig i Skåne och talgoxar, som alltså är icke-hamstrande generalister. Entitor kan gömma tusentals frön och larver på ett år. Talgoxar, å andra sidan, är välkända för sin förmåga att utnyttja många olika typer av födokällor genom sina innovativa födosökstekniker.

I papper I undersökte jag entitors spatiala (rumsliga) minne i ett fågelrum som är särskilt inrett för att fungera som arena för sådana studier. Det spatiala minnet är den typ av minne som gör det möjligt att memorera platser och rörelsevägar. Forskarvärlden är enig om att detta är den viktigaste mekanismen för hur spridningshamstrare kan hitta tillbaka till sina gömmen. I försöket lät jag entitor att gömma fem frön i arenan där det fanns 100 möjliga hamstringsplatser. När de lämnat arenan drog jag ner tyglappar över hålen så att varken hål eller eventuellt innehåll var synliga. Sedan fick titorna, antingen fem eller 24 timmar senare, leta efter sina gömmen. De hittade drygt 40 % i de 10 första tittarna vilket är i mycket stor överensstämmelse med andra liknande försök. De flesta fågel intresserade människorna är övertygade om att hamstrande fåglar har mycket bättre minne än de själva. För att undersöka om detta verkligen stämmer testade jag också människor i samma uppgift. Trots att hamstring av solrosfrön kan verka helt meningslöst för oss människor, var människorna mycket bättre än titorna. Eftersom människorna hittade de flesta fröna direkt blev framgången under de första tio tittarna ett meningslöst mått. Människorna hittade nämligen 80 % av gömmena på de första fem tittarna. Titorna klarade ungefär 20 % på de första fem tittarna.

Eftersom entitor har ett dokumenterat välutvecklat spatialt minne vore det logiskt om de hade bättre minne än vi människor, särskilt i en uppgift som verkar irrelevant för oss människor. En möjlig förklaring är att titorna hamstrar och letar många gånger i samma 100 hamstringshål under en försöksserie. Detta händer ju aldrig i naturen, där de alltid hamstrar i olika gömställen. Det är möjligt att kvarvarande minnen av tidigare hamstring på något sätt försvårar memorering av nya gömmen, s.k. proaktiv minnesinterferens. Interferens betyder här ungefär störning och innebär alltså att titorna får svårare att bilda nya minnen på grund av upprepad testning i samma omgivning. För att undersöka detta lät jag i papper II entitor att gömma och leta efter frön i tre på varandra följande sessioner. Om det finns en sådan interferens, borde deras framgång minska över sessionerna. De har ju redan innan detta försök hamstrat flera gånger i arenan. Jag hittade ingen antydan till någon sådan minnesinterferens, titorna presterade i stort sett likadant i alla tre sessionerna.

Från och med papper III går jag över till den andra sidan av dikotomin och fokuserar på talgoxar. Det är välkänt att talgoxar i fält ofta stjäl mat av sina hamstrande släktingar. Eftersom talgoxar är mycket större än de hamstrande arterna gör de ofta detta genom direkt stöld när de kör bort den mindre arten. Jag ville undersöka om de också kan observera och memorera gömmenas position, på samma sätt som hamstrarna själva. På vintern, när maten knapp är skulle en sådan förmåga kunna ge talgoxar tillgång till hamstrade matförråd, fastän de inte själva hamstrar. Jag lät talgoxar sitta i en bur och observera entitor medan de gömde mat hamstringsarenan som för övrigt var likadan som under försöken med entitor. Det visade sig att talgoxarna hade förmågan att hitta titornas gömmen, både en och 24 timmar efter observationstillfället. Detta är imponerande eftersom det rör sig om observationsinlärning på avstånd, som nog är mycket svårare än memorering av egna gömmen.

Eftersom denna förmåga alltså är annorlunda än memorering av egna gömställen ville jag undersöka om förmågan är unik för talgoxen eller om den också förkommer hos de hamstrande arterna. I det senare fallet skulle den alltså troligen förekomma i hela mesfamiljen. I papper IV gjorde jag därför exakt samma försök som i papper III, men denna gång med en observerande entita i buren. Entitor visade inga tecken på någon förmåga att minnas gömställen som artfränder gjort. Detta tyder på att detta är en unik förmåga för talgoxen. Detta är logiskt eftersom ju titan redan har stora mängder egen hamstrad mat. Varför då försöka sig på det svåra konststycket att memorera andras gömmen? Detta innebär då att sådan specialiserad avståndsmemorering är unik och inte en gemensam förmåga hos mesfamiljen.

Inom mesfamiljen är könsskillnaderna mest tydliga hos talgoxen, med tydliga skillnader i beteende, utseende och social rang. Därför valde jag att undersöka om det fanns någon könsskillnad i förmågan till observationsinlärning (papper V) av entitegömmen. Intressant nog var talgoxhonorna mycket bättre på detta än hanarna. Antagligen är det så att de dominanta hanarna har förtur till mat i naturen. Honorna kan då tjäna mycket på att memorera var en entita gömmer och senare återvända när inga hanar är i närheten.

I papper VI fortsatte jag studierna av ev. könsskillnader i kognitiv förmåga hos talgoxar. Nu testade jag dem i en uppgift som kräver självkontroll, den s.k. den transparenta cylinderuppgiften. Strikt sett testar detta något som kallas motorisk självreglering, en förmåga som är nödvändig för högre former av självkontroll. I den här uppgiften måste djuren behärska sin första impuls att gå direkt på den synliga belöningen (en matbit), som ligger inuti en tvärställd genomskinlig cylinder. Om de förstår cylinderns natur ska de istället göra en omväg till någon av de öppna ändarna och ta belöningen den vägen. Det har tidigare visat sig att djur presterar bättre i detta test om de har erfarenhet av en genomskinlig cylinder. Därför indelade jag fåglarna i två grupper; de som hade erfarenhet av cylindern och de som inte hade detta. De erfarna fåglarna hade en genomskinlig cylinder (utan mat!) på botten av buren i tre dagar före försöket, medan övriga fåglar såg cylindern för första gången under testet. Talgoxar var bra på den här uppgiften i allmänhet. Jag hittade ingen genomsnittlig skillnad mellan könen men hanarna lärde sig denna uppgift ganska snabbt även utan tidigare erfarenhet av en genomskinlig cylinder. Honorna, å andra sidan, utförde den betydligt bättre om de hade tidigare erfarenhet av den transparenta cylindern och överträffade då erfarna hanar.

Sammanfattningsvis, hittade jag kognitiva skillnader mellan två olika arter som representerar två distinkta födosöksstrategier inom samma familj. Jag tror att de skillnader jag hittade beror just på dessa skillnader i vinterekologi mellan dessa arter. Jag hittade också bevis på kognitiva könsskillnader i talgoxar, vilket jag föreslår beror på den tydliga rangskillnaden mellan könen hos denna art.

Introduction

Combinations of various abiotic and biotic factors create numerous types of environments that differ in many aspects. Each type of environment comes with its specific challenges for the organisms that are living in it and different organisms thus have various types of adaptations to cope with the specific challenges that the environment brings. While these adaptations can be simple structural or physiological ones, they can also consist of complex behaviours that animals perform. Many behaviours that we observe in animals are evolved responses to specific situations or environmental conditions, and are often genetically "hard-wired" into the animals' brains (Ricklefs 2004). Such "hard-wired" behaviours are especially common when animals need to cope with regular environmental changes such as changing seasons, diurnal rhythms, etc. However, since most environments are to some degree dynamic and unpredictable, animals will often encounter novel situations that require plastic behavioural responses. Even though hard-wired behavioural responses may be essential, they will in many cases not provide the flexibility that animals need to overcome unpredictable conditions (Shettleworth 1998). Cognitive abilities play an important role in coping with such environmental unpredictability. Cognitive mechanisms, which include learning, perception, memorisation and decision making, frequently make it possible for animals to obtain, process, and store information from the environment in order to adaptively organize or modify their behaviour (Cook 1993).

Complex cognitive abilities has evolved separately in different taxa (Osvath et al. 2014). The brain structure that is responsible for complex or advanced cognitive traits in mammals is the prefrontal cortex (Luria 1966). Although the avian brain lacks this structure, it has been shown that some bird species can perform on cognitive levels on par with cognitively complex apes (Emery and Clayton 2004, 2005; Emery 2006). This means that although animals such as birds and mammals are distantly related, they may share many cognitive skills. In addition, different selection pressures may cause cognitive differences to emerge within the same taxa, and even within the same species (Thornton and Lukas 2012; MacLean et al. 2012). Existence of such diverse cognitive abilities makes it necessary to conduct comparative studies.

There has been considerable research on a variety of cognitive abilities within avian taxa. These studies in avian cognition have mostly focussed on two families; parrots and corvids. Members of these families possess many abilities that can be considered complex and comparable to primates (e.g Auersperg et al. 2011, 2014; Güntürkün and Bugnyar 2016; Kabadayi et al. 2016; Kabadayi and Osvath 2017). Although birds have a brain volume that is considerably smaller than mammals on average, it has been discovered that the brains of song birds and parrots possesses a higher neuron density than the average mammal brain (Olkowicz et al. 2016; Herculano-Houzel 2017). This could explain why birds seem to have the capacity to develop cognitive abilities as advanced as some mammals, even though their brains in general are smaller in absolute terms.

Although parrots and corvids are still the foremost focus of research in avian cognition, lately there has been an increase in the number of studies investigating cognitive abilities in small passerines, especially in the family *Paridae* (tits, titmice and chickadees). This family has a wide distribution from Western Europe across Asia to Western Altai in Central Asia, Northern Japan, South-West China, Burma, Africa and North America (Snow et al. 1998; Hoyo et al. 2007). During the non-breeding season, some members of the *Paridae* family live in social flocks consisting of many different species (Ekman 1989; Sasvári 1992).

Within the European members of the *Paridae* family there is a dichotomy in winter foraging strategies between specialist food-hoarder species (e.g. marsh tits, willow tits, crested tits) that rely on cached food on cold winter days when food is scarce, and generalist foragers that do not store food (e.g. great tits, blue tits). With no access to stored supplies, the latter species may frequently have to adopt foraging skills that can be described as innovative.

There have been very few attempts to compare the cognitive abilities of both sides of this dichotomy (Sasvári 1979; Sasväri 1985; Hilton and Krebs 1990). There are many studies that have investigated various aspects of food hoarding birds in this family, mostly focusing on spatial memory (for a review see Brodin 2010). The other side of the dichotomy, the cognitive abilities of the non-hoarders are less well-known, despite extensive studies from ecological and evolutionary perspectives, on topics such as such as life history, diet, dispersal, and social systems (Harvey et al. 1979; Cowie and Hinsley 1988; Ekman 1989).

Aim

In this thesis, I investigate several cognitive abilities in two members of the *Paridae* family; marsh tits *Poecile palustris* and great tits *Parus major*. These species represent the two sides of the foraging dichotomy since the marsh tit is a food-hoarding, specialist forager, and the great tit is a non-hoarding, generalist forager. I compare the cognitive abilities of these species in special tasks that are relevant to their natural foraging behaviours. I aim to answer the broad question of whether the dichotomy in foraging strategies in the *Paridae* family causes cognitive differences between its members. In addition, I take this comparative approach one-step further and investigate a possible within-species difference in cognitive performance; namely sex differences in great tits.

In **paper I** and **II**, I investigate the spatial memory abilities of marsh tits in a typical laboratory food-hoarding task. In addition, I compare spatial memory abilities in marsh tits to those in the most cognitively advanced (although, contrary to what was previously believed, not cognitively unique) species; humans. In **paper II**, I investigate whether memory interference affects the performance of marsh tits in laboratory conditions. In **paper III**, I shift the focus to great tits and investigate their observational spatial learning abilities. In **paper IV**, I test marsh tits in the same observational spatial learning task as I tested the great tits in **paper III** and compare their overall performance in this task to those of great tits. Then in **paper V** and **VI**, I focus on cognitive sex differences in great tits in observational spatial learning (**paper V**) and motor self-regulation task (**paper VI**). In this thesis, I aim to contribute to general understanding of the variation in cognitive abilities of these small passerines.

Study species

Marsh tits

Marsh tits are small scatter hoarding passerines (11-12 cm, 8.9-15 g) in the *Paridae* family. This Eurasian species primarily lives in deciduous woodlands and frequently occurs in marshy habitats (Gosler and Clement 2007). Swedish marsh tit populations primarily occur in the southern part of the country, especially in deciduous forests, but also in gardens. During the last decades, the number of marsh tits in Sweden has decreased substantially, even though the numbers currently seem stable (Ottvall et al. 2008). This species is sexually monochromatic. The length of the wing is commonly used for sexing as males are somewhat larger, thus they have longer wings (≥ 63 mm) than females (≤62 mm) (King and Muddeman 1995). Marsh tits live in pairs and have a tendency to stay monogamous as long as their partner is alive (Morley 1950). The pairs live in territories, which are often established by the males. Although it is not as common, it is possible to see solitary individuals in nature. These birds are mostly unpaired adults and juveniles who usually join mixed species flocks to forage (Morley 1953; Ekman 1989).

The marsh tits' diet changes according to food availability in their surrounding environment. They consume mostly insects and spiders in the summer months, whereas in autumn and winter they eat more seeds and nuts. As many other members of the *Paridae* family, marsh tits are specialized hoarders. They store food all year around, but the intensity of food storing is much higher between early September and late November than at other times of the year (e.g. Vander Wall 1990). Marsh tits store food items into holes in the ground, among leaf litter, under lichens and mosses, on trunks and branches of trees and under woodpiles (Ulfstrand 1962; Vander Wall 1990). An individual marsh tit can store up to 89,000 seeds in one year (Haftorn 1959). They primarily store seeds and nuts but many invertebrates are also commonly stored when available (Hoyo et al. 2007).

Food hoarding parids rely greatly on their spatial memory for cache retrieval. They are considered to possess superior spatial memory capacity compared to similar non-hoarding species, as remembering the locations of cached food can be the matter of life and death (Krebs et al. 1989; Hilton and Krebs 1990). Several field studies have shown that marsh tits are capable of remembering the precise locations of seeds they have stored (e.g Cowie et al. 1981; Stevens and Krebs 1986). Laboratory studies have provided even stronger evidence that marsh tits use spatial memory to recover cached food (e.g Sherry et al. 1981; Shettleworth and Krebs 1982).

Figure1.
Marsh Tit (*Poecile palustris*) territorial display, Northumberland, UK. Photograph by Roger Powell /© Nature Picture Library / Universal Images Group. Rights Managed

Great tits

The great tit is a non-food hoarding songbird, and the largest member of the *Paridae* family (12.5-14 cm, 11.9-22.1 g) (Gosler and Clement 2007). Male great tits are usually larger than females with longer wings and a thicker black "tie" on the chest area. This stripe is a very distinct visual characteristic that male great tits possess. Great tits are generalist foragers and they are good at exploiting a variety of food sources. They are common in both rural and urban areas in Europe, the Middle East, North Africa and Central Asia (Hoyo et al. 2007). They are well-known for their innovative foraging skills (Estók et al. 2010; Cole et al. 2011). Moreover, they are one of the few bird species that can use tools to forage in nature (Cramp and Perrins 1993; Gosler and Clement 2007).

Figure2.
Great tit perched in hawthorn tree during winter, England. Photograph by Mike Wilkes /© Nature Picture Library / Universal Images Group. Rights Managed

General methodology

I conducted all my experiments under laboratory conditions. This approach allowed me to modify the setup according to the cognitive ability that I was testing and control the environmental conditions. The use of an indoor laboratory also allowed me to isolate birds during the experiments and test them individually.

As I worked with wild birds, the captive situation could potentially be stressful for the individuals. Therefore, in the experimental facility we tried to simulate natural conditions as closely as we could.

The experimental facility

The laboratory in which we performed the experiments was a 5 m × 3 m × 2.6 m indoor room in the animal facility of the Biology Department at Lund University. Both light regime and temperature were controlled through a computer. During the experiments, the temperature was set at a constant 14^{o}C. The lights in the facility have a natural daylight spectrum with a one-hour dawn/dusk dimming function meaning that it is possible to simulate a natural light regime. The daylight cycle was set to 10 h light/14 h dark during the food hoarding and observational spatial learning experiments. The rationale behind this was that the food hoarding intensity of marsh tits peaks in September/October when days may be 10 h long. During motor self-regulation experiments, the daylight cycle varied between 10/14 - light/dark and 8/16 - light/dark in approximate accordance with the outdoor light regime.

The entrance door to the laboratory was situated in a corner of the room and surrounded by a 2 × 1 m glass booth, which was used as an observation booth (Fig. 1). The walls and the glass sliding doors between the observation booth and the experimental arena were covered with dark smoke coloured one-way glass that, in combination with the darkness in the booth, made it impossible for the birds to see an observer from inside the arena. Adjacent to the observation booth, at one of the long sidewalls, three shelves from floor to ceiling were mounted. On each shelf, two cages (60x60x40 cm) were placed for individual housing of the birds. In front of these shelves and parallel to the long wall, we had mounted a wooden wall consisting of a board from floor to ceiling. This board divided the birds housing arena from the rest of the room that was used as experimental arena. The observer in the booth could see both the experimental arena and the bird-housing arena whilst still being unobserved by the birds.

On the wooden wall, in front of each individual cage there were cage-sized doors that could be removed from their hinges. When the doors were removed, it was possible for the birds to have full view of the experimental room from their cage. Next to these doors, there were small slide shutters (white with a black frame in figure 1) that could be opened to the experimental arena. These shutters were connected to the cages by a plastic tube with 12 cm diameter. The shutters were remotely controlled and motor driven so that they could be opened and closed from the booth. The rationale for this setup was to minimise the stress that the birds would experience during the experiments by being disturbed and handled before experimental sessions.

Figure 3.
The Experimental room. The artificial “trees” that we used in **paper I,II,III,IV,V** on the right hand side and the birds’ housing area on the left hand side of the picture. The painted shapes on the walls served as landmarks for the birds on the above-mentioned studies.

Capturing and Housing of the Birds

My supervisor, Anders Brodin, and I captured marsh tits near Höör (55° 56’N, 13° 32’ E) and great tits near Höör and in Lund in southern Sweden by using mist nets and playback. Birds were ringed individually with both uniquely numbered aluminium rings and colour rings. The colour rings made it possible to identify birds individually in the laboratory. We sexed the marsh tits according to wing length measurements. When we sexed the great tits, we used both visual evaluation of the plumage patterns (especially the width of the black tie on chest) and wing length measurements. We kept the birds in the laboratory under permit M213-11 from Malmö-Lund regional ethical committee.

Transportation time from capture area to indoor animal facility never exceeded 30 minutes. During transportation, all birds were kept in individual cotton bags. After the birds had been brought into the laboratory, they were immediately transferred into individual cages, measuring 60 cm x 60 cm x 40 cm. The birds were kept in these cages during the rest of their stay in the laboratory except for during the experimental sessions. The birds that had been captured in the same location were placed together in the shelf where they could have visual and auditory contact with each other. In the cage, the birds had ad libitum access to a crushed nut mix that contained sunflower seeds, peanuts and hemp nuts. In order to give the birds opportunity to handle living food, we sometimes provided them with mealworms. We also provided them with a lard ball that contained seeds and animal fat. We added a commercial bird vitamin mixture in the birds’ drinking water and changed the water daily.

Memory

Memory is a fundamental function of animal cognition. Most animals possess some type of memory capacity to some extent. It allows animals to acquire and retain information from their surroundings and to retrieve it when it is needed (Shettleworth 2001). In other words, memory consists of representations of past experiences that are stored in the brain (Olmstead and Kuhlmeier 2015) for short or long time intervals. While short-term memory (frequently referred to as working memory) can retain information for seconds or minutes, long-term memory can be stored for hours, days or even a lifetime. Animals can modify their behaviour and solve a variety of problems that they encounter in a changing environment by using stored information about their past experiences (Shettleworth 1998). Moreover, memory is required when carrying out various routine tasks in an animal's life, such as responding to stimulus in an appropriate way, recognizing other individuals, or remembering the locations of food and water sources.

Spatial Memory

Spatial memory refers to the type of memory that makes it possible for an animal to acquire and store visual information from its surrounding environment (Shettleworth 1998). Animals, ranging from small insects to primates, may in many situations, depend on spatial memory for survival. Almost all natural environments have different stable objects and patterns that can be used as landmarks for navigation (Cheng and Graham 2013). Animals form memories of these landmarks and use them in various navigation tasks, such as returning to a home territory or to good foraging grounds or water sources, avoiding areas with high predation risk and remembering routes which they can move efficiently (Wasserman and Zentall 2012).

Scatter hoarding of food is a good example of how memorisation of landmarks can be utilized in order to survive periods of harsh conditions. Food hoarding allows animals to have access to food supply even under conditions when the availability of new food is low and there is much competition for food (Vander Wall 1990). Scatter hoarders cache food items in many cryptic places where they will be reasonably safe from scrounging competitors. By caching food, hoarders can have control over when to retrieve and consume the food. Scatter hoarders normally use their spatial memories of caching positions to retrieve them later (Krushinskaya 1966; Sherry et al. 1981; Vander Wall 1982; Shettleworth 1990; Vander Wall 1990; Brodin 2010).

Food hoarding

In nature, animals are more or less in a constant struggle to find food. There is much competition for food, and the abundance of food may vary both in daily and seasonal patterns. In order to cope with periods of low food availability, animals have evolved different adaptations such as hibernation, migration and territoriality (in the sense of exclusive access to its food). Food hoarding is considered to evolve under conditions of high variability in food availability in the environment (Vander Wall 1990). Food hoarding animals store food when it is abundant and consume it later when food is scarce. Thus, food storing is considered to be a behavioural adaptation that makes it possible to survive periods of food scarcity (Sherry 1985).

When hoarding, food hoarders collect food items and hide them from potential competitors for future use (Vander Wall 1990). Hoarding has evolved independently in many different taxa and there are two main strategies used by hoarding animals (Smith and Reichman 1984). In the previous section, I discussed scatter hoarding, a strategy where food is dispersed in many locations. Some food hoarding species, however, accumulate the stored food items as one big pile in a reasonably secure place. This strategy is called larder hoarding and it is primarily used by animals that can defend this larder (Vander Wall 1990). The focus in this thesis, however, will be only on scatter food hoarding.

Scatter hoarders do not usually attempt to defend their caches, as this would be an ineffective strategy when the caches are distributed over a large area (Vander Wall, 1990). As the density of cached food items in a specific area is usually low, random search for caches by scroungers will be rather inefficient. In such cases, the loss of few food items will be a negligible cost for hoarders (Smulders 1998; Vander Wall and Jenkins 2003; Brodin 2010).

Most bird species that store food are scatter hoarders and this behaviour is especially prevalent among winter resident birds at northern latitudes. Many species of scatter-hoarding birds make thousands of caches in their surrounding environments (Vander Wall 1990). These caches are usually cryptic or hidden under leaves, tree branches, lichens etc. Such concealment decreases the risk of losing caches to pilferers. However, it also makes it more difficult for hoarders to find their own caches. The most effective way to relocate scattered caches is probably to memorise their exact locations.

It has been repeatedly documented that food hoarding birds use spatial memory to relocate their cached food (e.g. Krushinskaya 1966; Sherry et al. 1981; Vander Wall 1982; Shettleworth 1990). The hoarding species in the *Paridae* and *Corvidae* families have been the subject of many spatial memory studies (Vander Wall 1990, Shettleworth 2003; Sherry 2006; Brodin 2010). Many species in these families store thousands of food items in autumn and relocate them later with a great accuracy by using their well-developed spatial memory. Some of these species can retain these memories up to a year (for a review see Brodin 2005). The hippocampus, a particular brain structure, has been shown to be especially important in turning spatial information into spatial memories (e.g Squire 1992; Krebs et al. 1996; Macphail 2002). It has been demonstrated that food hoarding species possess a relatively larger hippocampus than their non-hoarding relatives (Sherry et al. 1989; Krebs et al. 1989; Lucas et al. 2004). The importance of the hippocampus became clear in experiments when this structure was surgically lesioned from the rest of the brain (Krushinskaya 1966; Sherry and Vaccarino 1989). After this operation, the birds would still store but were no longer able to remember the locations of their caches.

Many animals store food for long intervals, for example from autumn to winter, which has clear benefits. However, storing may also be advantageous on a short-term perspective. Several dynamic programming models (McNamara et al. 1990; Brodin 1997; Pravosudov and Lucas 2001) have shown that food storing is also advantageous on a short-term perspective when; i) carrying energy as a fat reserve is costly (for example by increased predation risk), ii) the supply of non-stored food in the environment becomes unpredictable, iii) the supply of non-stored food in the environment rapidly decreases, and, iv) energy expenditure during night is unusually high.

In a game theoretical model, Andersson and Krebs (1978) showed under which conditions a hoarding strategy could evolve in a species. It will be superior to non-hoarding or scrounging strategies if i) hoarders gain more from hoarding than leaving the source for later consumption, and, ii) hoarders have a greater chance of recovering their own cache compared to conspecific individuals in their group.

In agreement with these predictions, many empirical studies have shown that parids gain fitness by storing their food for later consumption (e.g. Cowie et al. 1981; Stevens and Krebs 1986; Brodin 1992). Even though this theory is widely accepted, it has also been suggested that hoarding can sometimes evolve under less strict conditions, for example it may evolve despite a higher level of cache loss than postulated by Andersson and Krebs (Smulders 1998; Vander Wall and Jenkins 2003).

How accurately can marsh tits relocate their own caches?

The spatial memory abilities of marsh tits and their close relatives have been investigated from several perspectives. Some studies have focused on spatial memory longevity (e.g Hitchcock and Sherry 1990; Brodin and Kunz 1997), others on the memory of the content of caches (e.g Sherry 1984), and the significance of landmarks for retrieval of the caches (e.g Herz et al. 1994)

Box 1.

Setup for Food Hoarding and Observational Spatial Learning Experiments

During the food hoarding and observational spatial learning experiments, we positioned 10 wooden boards that were 2.5 m in height, 4.5 cm deep and 9 cm wide, which we used as caching substrates in the experimental arena (the X-s in Figure 1). These "artificial trees" were placed along the wall opposite the birds housing arena. The boards were placed with 30 cm distance between them. On the boards and the walls between them, we painted different patterns such as circles, bars, waves etc. in red, black grey and green colours. Our intention was that these patterns should serve as unique landmarks for the subjects of the experiments. On the side of each board facing towards the birds' housing arena, we drilled 10 caching holes. The holes were spaced 15 cm vertically apart from each other and the lowest hole was 20 cm above the floor. Five centimetres below each hole, we had mounted a wooden stick that served as a perch for the birds. Right above each hole a piece of cloth was nailed so that it would cover the hole entirely but also could be easily moved to both sides by the birds. This system made it possible for us to make the hole and its content fully or partially visible, or to conceal it completely.

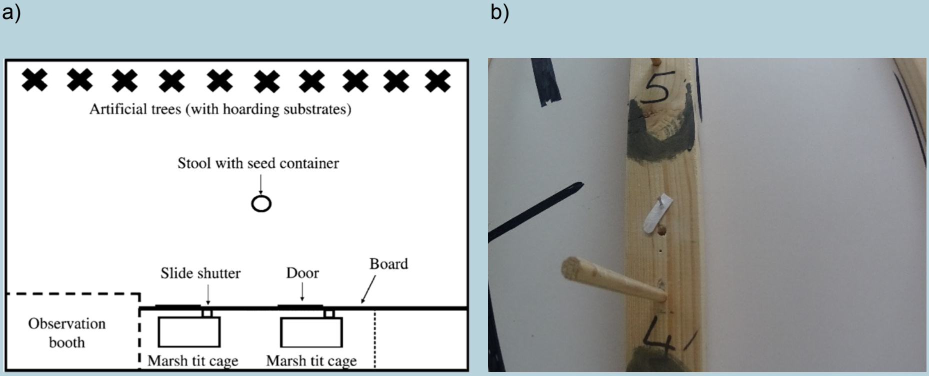

Figure B1.1:
a) The experimental room consisted of an observation booth, a bird housing area and an experimental arena with 10 wooden boards used as caching substrates. In the centre of the arena there was a stool with a seed container. b) A caching hole and a perch on an artificial tree.

Early studies that investigated memory capacity in food hoarding birds were mostly carried out in the field (Swanberg 1951; Tomback 1980). These studies, however, lacked control procedures such as colour banding of individual birds, and neither caching nor retrieval were directly observed. Even though the memory accuracy of cache recovery has been recorded in many ways (Shettleworth and Krebs 1982, 1986; Shettleworth 1990; Hitchcock and Sherry 1990; Clayton 1993; Healy and Suhonen 1996; Brodin and Kunz 1997), the proportion of the caches recovered have rarely been strictly recorded.

In **paper I**, we investigated how accurately marsh tits can relocate their cached food after 1 and 24 hours retention intervals. Accuracy here means the memory of the precise position, not the longevity of the memory. In order to test this we captured 12 wild marsh tits outside Höör (southern Sweden) and brought them into the animal facility at the department of biology. We used a laboratory set-up that was designed to be as similar as possible to the set-ups in previous laboratory studies on food hoarding in small parids (Box1). The birds were allowed to store five seeds into caching holes. Either 5 hours or 24 hours later, we released the birds back into the experimental area and allowed them to search for the caches. The results revealed that both 5 and 24 hours after storing, around 40% of the caches were successfully retrieved in the first ten attempts when the birds had stored five seeds in 100 available sites. Our results are in accordance with previous studies that used similar experimental approaches to test spatial memory ability in this species (Shettleworth and Krebs 1982; Shettleworth and Krebs 1986; Clayton 1993; Healy and Suhonen 1996).

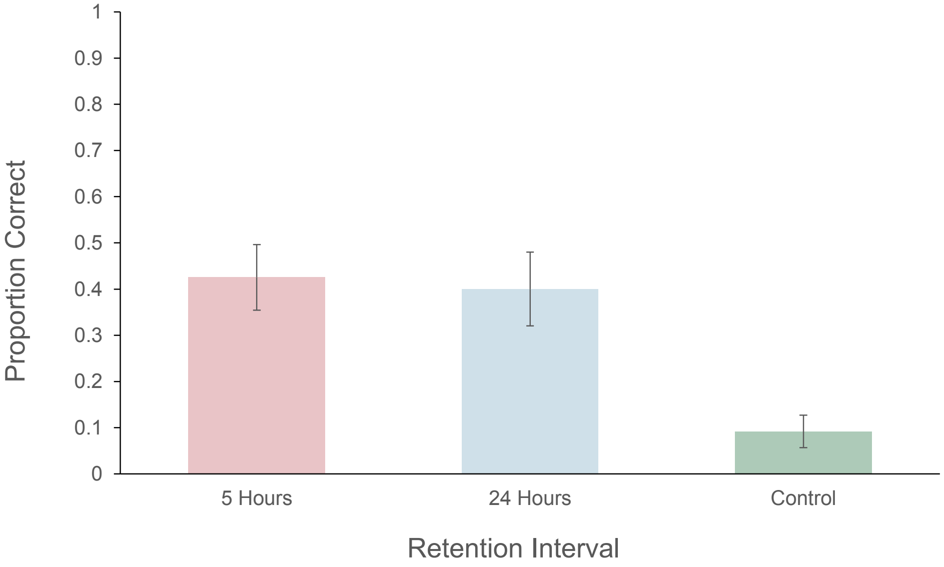

Figure 4.
The proportion of correct looks in the first 10 attetmpts after 5 hour and 24 hours retention intervals . The error bars are 95 % confidence intervals

During the retrieval sessions, the marsh tits would typically perch on a position in the tree after they had been released into the experimental arena. One may assume that if they remember the precise cache locations, they would first go for the closest cache. First, we measured the distance from the first perch used by the bird to the next hole inspected, and then to the first correct hole visited. The distance between the "starting-perch" and the next hole inspected was shorter than the distance between the "starting-perch" and first correct hole visited. It is reasonable to assume that the marsh tits must remember at least the first cache they retrieved. The fact that they inspected "incorrect" holes on their way to the first cache implies that they may be inspecting any holes that happen to be on their way to a remembered cache. However, the distance between the starting-perch and the nearest non-investigated correct hole, was significantly shorter than the distance to the first correctly visited hole, meaning that marsh tits did not start by going to the caches that was closest to them. This suggests that the marsh tits may remember only some caching sites, or, they may prefer to retrieve some caches before others. Another possibility is that marsh tits may remember but still leave some of their caches for later consumption.

Humans vs. Marsh Tits – Who has a better spatial memory?

In the Descent of Man (1871), Darwin claimed that the difference in cognitive and behavioural capacities between humans and other animals is a product of evolutionary processes. He argued that the origin of human intelligence can be traced back to our common ancestors with other animals. Today it is generally accepted that humans and non-human animals have a variety of cognitive abilities in common. Cognitive and behavioural studies on various taxa, from vertebrates to primates, have shown that many species possess cognitive skills that previously only humans were thought to possess (Gould 2008).

One cognitive ability that has been studied and compared between different species is spatial memory. Some studies have compared spatial memory in humans and non-human animals attempting to investigate to what extent they have developed in parallel (Squire 1992; Gentner 2007; Haun et al. 2011). As mentioned above, scatter hoarding birds are considered to be a model system for studies of spatial memory (Shettleworth 2003; Sherry 2006; Brodin 2010). However, even though it is well known that food hoarding birds have a well-developed spatial memory, it has not been explicitly studied how successful they are compared to humans.

Modern humans (*Homo sapiens sapiens*) have advanced spatial cognition abilities that presumably are more advanced than in early human species (Wynn 2002). Recently, it has been suggested that the mobility skills of humans, which is the result of our advanced spatial cognition abilities, was the key factor of human survival in Late Pleistocene, and that the Neanderthals' apparent sedentary life (presumably due to less developed spatial cognition abilities) may have been an important reason for their extinction (Burke 2012). Using spatial memory, modern humans can successfully recognize locations, memorise landmarks, learn pathways, estimate distances and create mental maps of their surroundings (Allen 2004).

Like food hoarding birds, humans can also use landmarks and cues to orient themselves. Even though the most important cues are gained through egocentric experiences (location of the object in space relative to one self), humans are also capable of using allocentric cues (location of the object in space relative to another object) (Klatzky 1998; Allen 2004).

In addition to retrieval accuracy of marsh tits, in **paper I** and **II**, we also investigated the spatial memory ability of humans compared to marsh tits. We tested 12 human subjects in the same set-up and compared their performance to that of the marsh tits. The most important difference in the experimental procedure compared to the marsh tits was that human subjects cached the seeds into the caching location that were pre-determined by the experimenter by Monte Carlo lottery (drawn blindly from a box with 100 different tickets). The rationale behind this procedure was to prevent humans from caching in some systematic manner, which may make it easier to memorise the locations. Food hoarding birds such as marsh tits have specialised spatial memory abilities and they have been suggested to be able to memorise the locations of hundreds or even thousands of different caches. Therefore, we (and also the experimental human subjects) expected the marsh tits to perform better than the humans in this task. Humans, however, performed almost perfectly and were able to relocate almost all five caching positions within the first five attempts with an accuracy of 87% and 88% after 5 hours and 24 hours respectively. Since humans were so accurate in their first five looks, the success in the first ten looks became somewhat meaningless as a measure to compare. This is remarkably high when compared to the performance of marsh tits that relocated 25 % of the caches in the first five attempts.

There may be several reasons for humans' superior performance in this task. Our setup may be unnaturally regular and thus easier for humans to memorise. Hence, humans may have memorised the locations of caches in some systematic mnemonic way, rather than memorising landmarks. Still, we tried to prevent this by trying to convince the human subjects to specifically use the landmarks rather than some other type of memory.

Does memory interference influence the accuracy of marsh tits and humans?

Food hoarding birds create numerous new caches, especially in autumn, and as a result, they form numerous new memories during their daily foraging routine. Even if species such as marsh tits are specialized in memorising many different caching locations, it is possible that old memories will interfere with the formation of new ones. As old memories are recalled this may create an effect of newly acquired memories being more frequently and rapidly forgotten. Such interference by previous memories is called proactive memory interference (PI) and it has been suggested to be frequent in food hoarding birds (Wright et al. 1986). It has also been shown that more recently acquired memories may hamper recall of previously acquired memories (retroactive interference) (Gaffan 1992). However, in this thesis I did not focus on this type of memory interference.

Besides food hoarding birds, proactive memory interference have been demonstrated in a variety of animals such as rats (Olton and Samuelson 1976; Olton and Paras 1979; Roitblat and Harley 1988), pigs (Mendl et al. 1997), humans (Keppel and Underwood 1962; Henson 1998) and some other primate species (Jitsumori et al. 1988).

A study on Clark's Nutcrackers *Nucifraga columbiana* (Lewis and Kamil 2006) found clear evidence for memory interference, as the birds made fewer errors when they were presented with only one sequence of locations. Similarly, Olson et. al (1995) compared two specialized food hoarding corvids (Clark's Nutcracker and Pinyon jay *Gymnorhinus cyanocephalus*) and two moderately specialized food hoarding corvids (Scrub jay *Aphelocoma coerulescens* and Mexican jay *Aphelocoma ultramarina*) in a spatial memory task, by using touch screens. The expected outcome of the study would be that that the degree of caching specialization would correlate with the performance of the birds in spatial tasks. The pinyon jays seemed to be more prone to suffer from proactive memory interference as the nutcrackers outperformed them on this task. The Pinyon jays seemed to suffer from the repeatedly presented operant tasks they experienced every day. Thus, an experiment on four species of corvids showed that in food hoarding birds more generally, it is common to see some evidence of memory interference.

In another experiment, black-capped chickadees *Poecile atricapillus*, close North American relatives of the marsh tits, were presented series of up to three items that differed in colour and shape (Hampton et al. 1998). They were then required to peck at the last item they encountered in the series. The chickadees showed clear memory interference in these matching tasks. However, similar studies conducted on marsh tits have failed to replicate these results (Healy and Krebs 1992; Healy and Suhonen 1996).

The results in **paper I**, that humans were able to relocate almost 90 % of the caches they had hidden 5 hours earlier while marsh tits only recovered 25 %, was surprising to us. Hence, we tried to understand if our laboratory set up in some way could make the birds less successful than they would be in nature. In this experiment, the birds cache and retrieve many times in the same sites in the same experimental room. In nature, conditions are very different as marsh tits only cache once in a particular site. As a result of repeated caching and retrieving sessions in the same sites, we hypothesized that, memories from previous sessions in some way may interrupt the formation of new memories. If there is such a proactive memory interference, the prediction is that retrieval success should decline over repeated sessions.

Hence, we designed an experiment to investigate whether the low retrieval success of marsh tits could be explained by such memory interference in these type of experiments **(paper II)**. Once more, humans were included to the experiment for comparison. In this design, we allowed marsh tits and humans that had no prior experience of the arena, to cache and later retrieve in three repeated sessions (cache-retrieve-cache-retrieve, etc.). However, the retrieval performance of neither humans nor marsh tits changed over sessions. Marsh tits still re-located around 25 % of the caches in the first five attempts. In humans, the retrieval success was similar over sessions, around 90 % in the first five attempts. In conclusion, we found no evidence that the performance of either marsh tits or humans should have been influenced by proactive memory interference.

It is indeed possible that marsh tits may experience memory interference in different tasks to those that we conducted. In addition, we may have found memory interference if we had continued with additional sessions after the third one. As in most cases, our results are specific for our setup and experimental design. Therefore, it is hard to draw strong general conclusions regarding memory interference in marsh tits from our study.

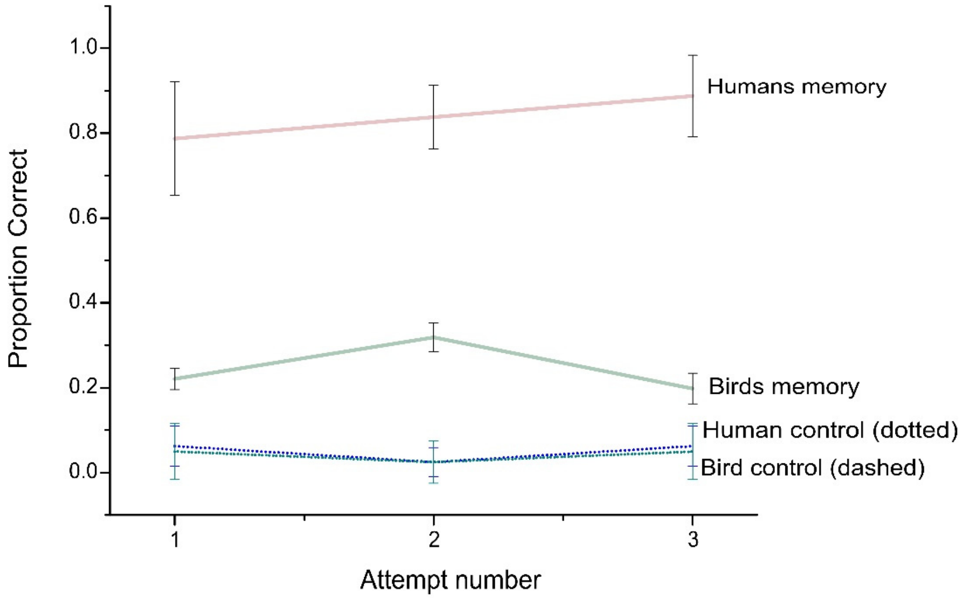

Figure 5.
The proportion of correct attempts in the first, second and third sessions by humans and marsh tits (solid curves). Control sessions of humans are shown with dotted curve, control sessions of marsh tits are shown with dashed curve. Error bars are 95% confidence intervals. Redrawn from **paper II**

Why then does a bird, which caches thousands of seeds in a season in nature, fail to relocate so many caches in our test? We have already discussed some possible explanations to this question in the previous section. Another possible explanation could be that the laboratory conditions are so different from natural conditions in various aspects and this, in some way, may have affected the birds' motivation to memorise cache locations. It is also possible that, although marsh tits store many seeds in nature, they do not memorise every single cache. Marsh tits are territorial during winter (Ekman 1989) and by storing more than they memorise, they can increase the general food availability within their territory.

Observational learning

Most animals change their behaviour as a result of information they have gathered from their environment (Shettleworth 1998). This information may also be acquired socially, by observing how other animals behave. Observational learning is a process that makes it possible to transmit information about a behaviour, or the behaviour itself, from one animal to another (Heyes and Galef 1996). By learning through observation, animals can gain important information faster and avoid the cost of learning through asocial means, such as trial and error (Laland 2004). Previously it was thought that primates were the only animals to possess social cognition, however later studies documented many instances of social cognition in many vertebrate species, including the spread of novel behaviours in populations through observational learning (Heyes and Galef 1996; Shettleworth 1998; Pearce 2013). Although it is frequently adaptive to use information acquired through observational learning, some claimed that this type of learning can be costly (Laland 1996; Giraldeau et al. 2002); and if the costs of learning are greater than its benefits, animals will not develop a cognitive capacity for a such mechanism (Dukas 1998, 1999).

In order to survive, animals have to acquire the necessary information to avoid predators, find the best grounds for feeding, select diet, and in some cases, they have to learn to communicate such information. It is almost impossible for juveniles to accomplish any of these activities on their own (Galef and Laland 2005). Although some behaviours can be inherited, much information need to be acquired from their surroundings and other individuals. Therefore, observational learning plays an important role in the life history of many animals. For example, in a cross-fostering experiment in the field, great tits that are reared by blue tit *Cyanistes caeruleus* parents behaved more similarly to blue tits while foraging, and vice versa, suggesting that information that is acquired early in life determines the behaviour in adulthood (Slagsvold and Wiebe 2011).

In addition to such studies of observational learning in early life stage, there are many studies that have examined the observational learning abilities of adults, also in birds (Heyes and Galef 1996; Lefebvre and Boogert 2010; Pearce 2013). In particular, great tits have been the focus of many of these studies. For example in Britain, they are infamous for opening milk caps with their beaks to reach the cream on the top of the milk (Fisher and Hinde 1949). This behaviour is believed to have originated in one group and spread throughout the population (Sherry and Galef 1984; Lefebvre and Boogert 2010). This shows that this species are capable of observing conspecifics and copying the novel foraging behaviours that they have observed. Moreover, one recent study has shown that their social learning tendency can lead to conformity within the population where all individuals may adopt the same approach to solving the same problems even though there are multiple possible solutions (Aplin et al. 2015).

Observational spatial memory

In the previous sections, I have discussed spatial memory somewhat generally. In this section, I will focus more specifically on observational spatial memory and learning, which requires a combination of observational learning and spatial memory abilities.

In this thesis, observational spatial memory has a specific meaning: it refers to learning of the location of caches through observation of the act of caching performed by conspecifics or interspecifics (Scheid and Bugnyar 2008). There are number of studies suggesting that birds – mainly within the corvid family – can observe conspecifics or interspecifics caching, and learn the exact locations of these caches (e.g Bednekoff and Balda 1996a; Bugnyar and Kotrschal 2002; Watanabe and Clayton 2007).

Members of the corvid family are known for their advanced cognitive skills and they possess a highly developed spatial memory for the caches that they have made themselves (Vander Wall 1990). When it comes to observational spatial memory, however, there is a considerable variation within the family. When given the opportunity to observe caching conspecifics, pinyon jays could memorise the cache locations accurately (Bednekoff and Balda 1996a; Dunlap et al. 2006). Although not as accurate as pinyon jays, Clark’s nutcrackers and Mexican jays were also able to memorise the locations of caches made by conspecifics when tested in the laboratory set-up (Bednekoff and Balda 1996b). Another corvid species, the grey jay *Perisoreus canadensis*, failed to memorise the positions of caches in a similar experiment (Bunch and Tomback 1986). The cognitive skills of the common raven (*Corvus corax*) is often considered on par with that of non-human primates (Bugnyar 2013; Kabadayi et al. 2016; Kabadayi and Osvath 2017). In two studies conducted in large enclosures, the common raven could memorise the locations of caches made by other ravens that they observed caching (Heinrich and Pepper 1998; Bugnyar and Kotrschal 2002).

Such a cognitive ability can be considered advanced, as it requires understanding of allocentric space. For example, when a bird hides a food item itself it only needs to perceive the environment from its own point of view. It then gets the opportunity to observe the site from various angles. Typically, the food hoarding parids perform a close visual inspection of the cache, usually with one eye, after making the cache. This process allows the bird to perceive location of the cache and landmarks around it from its own perspective. Such memorisation, when the animal determines spatial relations relative to its own location, is said to occur in egocentric space (Klatzky 1998). Most animals have some understanding of the egocentric space and are able to acquire and update spatial representations from an egocentric perspective. Allocentric space, on the other hand, is the point of view that is not visually experienced by the animal itself. Animals have to reconstruct the spatial information that they acquired through the egocentric process, through another animal or object's vantage point (Klatzky 1998). For example, during observational spatial learning, the bird has to have the ability to perceive the area and surroundings of the cache location from another individual's point of view. When the observer gets the opportunity to approach the area, it is likely that the approach will be from another angle than previously observed. Therefore, the animal has to assess the position of the cache according to this new angle. This makes memorisation of other individual's caches more complex than the memorisation of one's own caches.

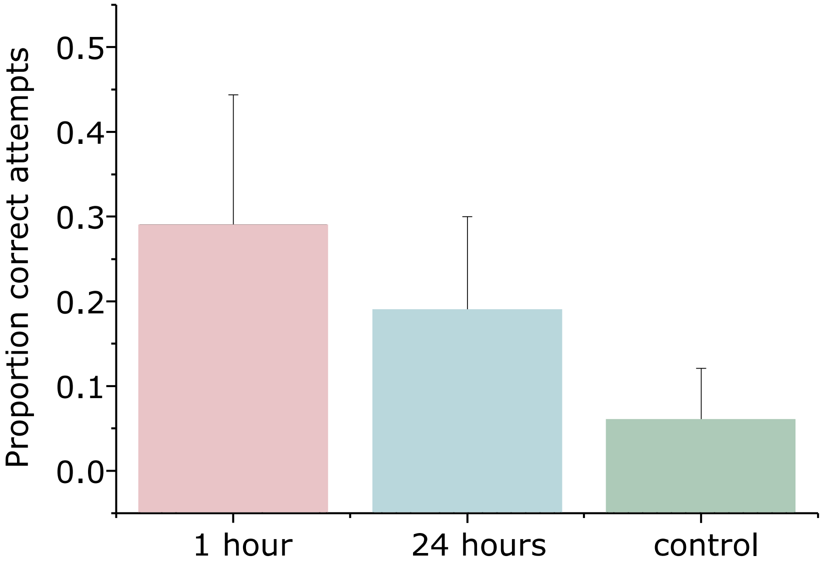

Figure 6.
The proportion of correct looks in the first ten attempts after 1 and 24 h. The error bars are 95 % confidence intervals. Redrawn from **paper III**

How do you survive among food hoarders, if you are not a food hoarder?

So far, much of the discussion has focused on the food hoarding side of the foraging dichotomy within the *Paridae* family. Now I will turn to the other side, that of the non-hoarding generalists. It is logical to assume that these species must possess mental capabilities that make it possible to survive the same conditions that the food hoarder specialist can overcome by caching excess food.

In the *Paridae*, both food hoarding and non-hoarding species will join mixed foraging flocks, except for during the breeding season (Morley 1953; Ekman 1989). As group living can benefit individuals in terms of predator protection (Ekman 1987) and by facilitating locating food sources (Krebs et al. 1972), for food hoarding species, it may be costly if it increases the probability of cache loss due to pilferage. For example, despite living in the same wintering flocks, it is reported that willow tits and crested tits segregate their caching sites due to risk of interspecific cache pilfering (Alatalo 1991). Field observations and studies suggest that cache pilferage occurs commonly among parids (Gibb 1954; Brodin 1993; Brodin and Ekman 1994; Gosler and Clement 2007). There are various pilfering strategies that are adopted by pilferers, such as random search of the caches and pilfering through olfactory means (Dally et al. 2006). However, these strategies may be either ineffective or require very specific conditions to be in place.

Observational learning of the cache locations of other individuals can be more effective and a safer way to pilfer food. In a mixed flock where food hoarding and non-hoarding species live side-by-side, there will be many opportunities for non-hoarding members, such as great tits, to observe food hoarding members, such as marsh tits, while they are caching food. If the caching site has been memorised the observer can, and will, steal the food after the hoarder leaves its cache.

To explore this idea, in **paper III** we tested great tits for their observational spatial learning abilities. We allowed a marsh tit to store five seeds while a great tit was observing them. Then, we allowed the great tit to enter the arena after a retention interval of either one hour or 24 hours. We allowed the great tits to search for caches for a maximum of five minutes. Before each search session, we randomly removed two of the five seeds to reduce the risk of satiation effects that could reduce the bird's motivation to forage. As control, we allowed great tits to search for caches made by a marsh tit in a session that the great tit had not observed.

Great tits relocated almost 30 % of the observed caches after the one-hour retention interval and 20 % after the 24-hours retention interval. Only 7 % of the caches were located in the control sessions when the great tits had not observed marsh tits making the caches. This implies that great tits are capable of observational memorisation through observation and the successful retrievals were not the result of some other process, such as random search. The mean number of searched locations were higher in the control sessions than in the experimental sessions. Therefore, this difference showed that great tits did not search in a seemingly random way during the observed sessions as opposed to the unobserved control sessions.

In Sweden, especially in the winter months, great tits live in an environment that has varying availability of food. On a cold and short winter day, it might be crucial to have access to food that has been cached by food hoarders. Our results are remarkable for three reasons. First, great tits are not food hoarders themselves and they have a smaller hippocampus relative to their total brain volume, compared to their food-hoarding relatives (Garamszegi and Eens 2004). Second, as I discuss above, the process of memorising others' caches is different compared to when memorising one's own caches. It may require understanding of the allocentric space, which makes observational spatial memorisation a cognitively more complex ability than memorisation of own caches. Third, heterospecific observational learning is rare in nature and, to my knowledge, this is the first demonstration of observational spatial learning in birds outside the corvids.

Is observational spatial learning common in *Paridae*?

It is remarkable that great tits can learn cache locations of marsh tits and keep this memory up to 24 hours, but does this ability also occur in marsh tits? Is such a complex cognitive ability just possessed by great tits, as innovative non-hoarding specialists, or is it common among all parids? After all, observational learning is a common cognitive ability and most passerines have observational learning ability to some degree, as they copy behaviours of others and learn from their parents (Sasvári 1979; Heyes and Galef 1996; Slagsvold and Wiebe 2011).

Black-capped chickadees, have been tested for observational spatial learning in a similar set up to ours (Baker et al. 1988; Hitchcock and Sherry 1995). These studies showed that although this species has a good spatial memory for the position of its own caches, failed to memorise the caches made by conspecifics.

In **paper IV**, we tested marsh tits for their observational learning ability using the same setup as that of our study of observational spatial memory in great tits. It is important to note that here we do not test whether marsh tits pilfer conspecifics' caches. If a marsh tit encounters a cache that belongs to another individual, it is very likely that it will pilfer it (Stevens and Krebs 1986; Brodin and Ekman 1994). Here we investigated, if they can observe hoarding conspecifics and memorise the precise positions of these caches in the same way as great tits.

Marsh tits did not appear to be able to memorise the positions of caches made by conspecifics, neither after the one-hour retention interval nor after the 24-hours interval. These results were in accordance with the results in two similar previous studies on black-capped chickadees (Baker et al. 1988; Hitchcock and Sherry 1995). One important study has shown that all parids are capable of observational learning, but that the great tit is much better at this than the marsh tit (Sasvári 1979). It is thus possible that observational learning and food hoarding are two competing foraging strategies that require special adaptations, for example in the brain. If this is true, small wintering birds such as parids, could be either skilled food hoarders or skilled observational learners as it is probable that there are trade-offs between such cognitive abilities. Non-hoarding great tits are known for their innovative foraging skills and these skills tend to spread within a population (e.g. Aplin et al. 2015). This indicates that great tits are very good at learning from conspecifics, and our results, in combination with previous studies, indicate that they are also good at learning from other species (Sasvári 1979; Sasva et al. 1998). It is therefore very likely that non-hoarding parids are better at using observational learning strategies to forage than their hoarding relatives. Although we have failed to demonstrate that marsh tits can use observational learning in the same way as great tits, this, of course, does not mean that they do not have observational learning ability.

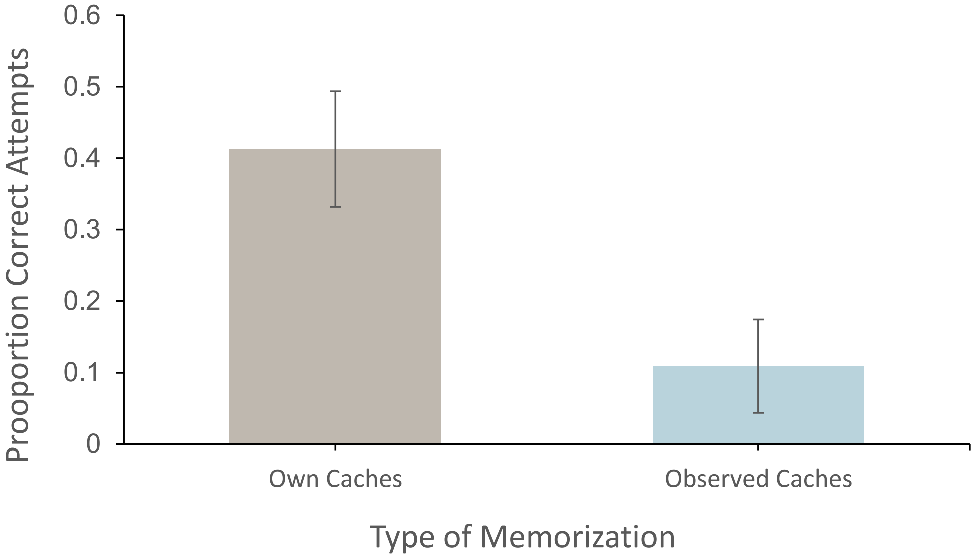

Figure 7.
The proportions of correct attempts in the first 10 looks when marsh tits searched for their own caches and caches they had observed other individuals making. The error bars are 95 % confidence intervals

Cognitive sex differences

Cognitive skills often vary between species. Similar environmental constrains may lead to various cognitive adaptations which allow different animals to solve essentially the same problem by using different approaches. Cognitive variation within species, however, is not as common. Although males and females of the same species often show pronounced differences in their morphology (Gosler 1986; Shine 1989; Gosler and Clement 2007), physiology (Tschirren et al. 2003; Carere and Van Oers 2004) and behaviour (Harvey et al. 1979), it is not common to find much variation in their cognitive abilities. However, over the last two decades, the interest in the variation between the sexes within species has increased and many examples of such differences in cognitive ability have been discovered (Halpern 2013; Miller and Halpern 2014).

In humans, there are well-established differences in cognitive performance between males and females. Males tend to perform better in spatial tasks (Astur et al. 1998; Dabbs et al. 1998; Moffat et al. 1998) and females tend to outperform males in verbal tasks (Bradshaw and Gates 1978). However, these differences can be quite small and may sometimes depend on the experimental design (Voyer et al. 1995; McBurney et al. 1997; Weiss et al. 2003; Hausmann et al. 2009).

In other mammals, however, sex differences can be pronounced. Most of the studies in mammals have focused on spatial cognition (Gresack and Frick 2003; Perdue et al. 2011). The majority of these studies have demonstrated that males perform better in spatial tasks than females (Mishima et al. 1986; Gaulin and Fitzgerald 1989; Gaulin et al. 1990; Jones et al. 2003). There are various hypotheses that seek to explain such differences between the sexes of the same species, including the effect of hormones (Williams and Meck 1991; Gaulin 1992), sex differences in dispersal (Jones et al. 2003) and sex differences in size of the territory (Jones et al. 2003; Perdue et al. 2011).

Studies of possible cognitive sex differences in birds have also mostly focused on spatial cognition. However, unlike mammals, these studies have in general not found any consistent male advantage in spatial ability. On the contrary, in some bird species, females seem to perform better in spatial cognition tasks than males (Petersen and Sherry 1996; Clayton et al. 1997; Guigueno et al. 2014).

Is there a Sex Difference in Observational Spatial Learning Ability in Great tits?

In **Paper V**, we discussed potential sex differences in observational spatial memory in great tits. In many animal species, males and females hold different positions within the social hierarchy. In great tits, males are generally dominant over females, and this rank difference potentially drives females to adopt a strategy that allows them to exploit food sources when males are not present in the area. However, it is not always possible to stay in the vicinity of the food source, as there are many environmental factors, such as predation risk, that can lead females to leave the area prematurely. Hence, it is possible that female great tits can benefit greatly from an ability to memorise the locations of the food source and come back later when their male counterparts are not in the area.

In our study, we showed that females were able to memorise the cache locations of marsh tits and retain this memory at least up to 24 hours (and possibly much longer) whereas males were not as good. As males are dominant over females they have prior access to food and can easily displace female great tits from food sources. Because of this, female great tits can probably benefit more than males from remembering cache locations of marsh tits. First, females can increase their access to food by using this ability when other food sources are dominated by male great tits. Second, females can choose not to retrieve a food item when a male is nearby. After the males have left, females can then retrieve the food without a risk of displacement.

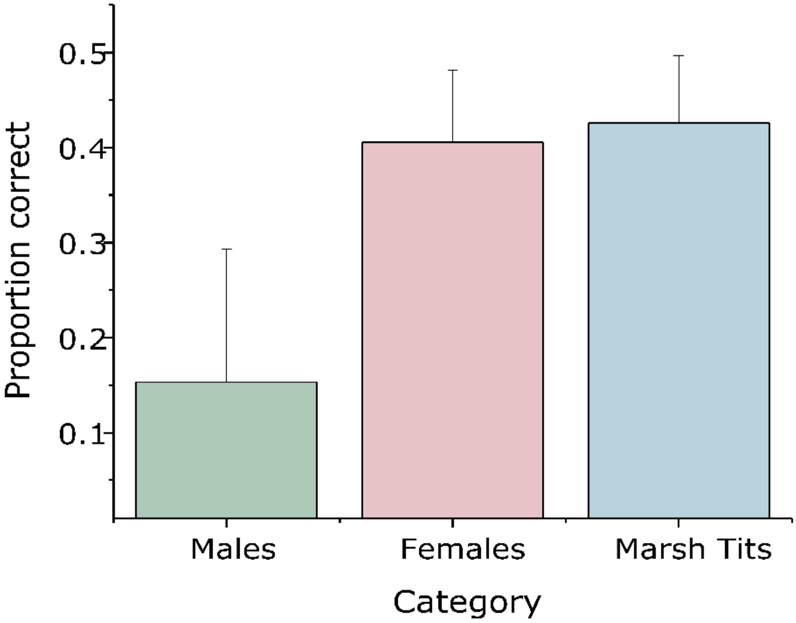

Figure 8.
The proportion of correct attempts for male and female great tits in the first ten looks after observing a caching marsh tit, compared to the proportion of correct looks for the caching marsh tit itself. The error bars are 95 % confidence intervals

Is there Evidence for Sex Difference in Motor Self-Regulation in Great Tits?

Inhibitory control is commonly defined as the ability to override immediate temptations for more appropriate behaviour (Diamond 2013). Being a core component of executive functions, inhibitory control is an essential ability for many complex cognitive processes, such as decision making and planning (Osvath and Osvath 2008; Diamond 2013; Kabadayi et al. 2016). Inhibitory control is an umbrella term that comprises diverse processes ranging from motor inhibition to self-control. Whereas motor inhibition, also called motor self-regulation, involves inhibiting a prepotent motor response to select a more appropriate behaviour, self-control involves a decision between two options that are separated in time: e.g. declining an immediate but a smaller reward in favour of a later but a larger reward (Beran 2015). Since motor self-regulation is an underlying cognitive mechanism that supports higher forms of self-control as well as other complex cognitive processes, its comparative investigation can yield important insights on the evolution of complex cognition (MacLean et al. 2014). One way to test for motor self-regulation is to use “the transparent cylinder” test. In this test, the animal is first trained to take food that is placed at the centre of an opaque cylinder that has openings in both ends. After training, the opaque cylinder is replaced by a transparent one, usually positioned perpendicularly to the direction of the animal’s approach. The animal passes the test if it takes a detour to the opening of the cylinder and retrieves the food. If it attempts to reach for the food directly through the transparent wall of the cylinder, it fails the test. This test measures whether the animal can inhibit the prepotent motor response for directly reaching for a visible reward behind a barrier, and instead take the detour that was learned with the opaque cylinder.

In a comprehensive study, McLean et al. (2014) tested 36 species of mammals and birds in the transparent cylinder test. The authors claimed that absolute brain volume is the best predictor variable for motor self-regulation ability in animals, at least in mammals and birds. Of the species that MacLean and colleagues (2014) tested, however, only seven were bird species. Of these seven species, four scored better than 50 percent in the test; the western scrub jay *Aphelocoma californica* (76.7%), the Eurasian jay *Garrulus glandarius* (58.3 %), the zebra finch *Taeniopygia guttata* (52.2%) and the orange-winged amazon *Amazona amazonica* (50.8%). This rather low general performance in birds, however, has recently been challenged by Kabadayi et.al. (2016) who tested three corvid species, ravens *Corvus corax*, New Caledonian crows *Corvus moneduloides* and jackdaws *Corvus monedula*. Kabadayi et al. showed that these corvids can perform this task on a similar level as the great apes (between 90 and 100%) despite having a much smaller brain volume. The authors also found that the relative brain volume as well as the absolute brain volume was a significant predictor of motor self-regulation ability within birds. A recent study in our laboratory demonstrated that great tits can score up to 80 % in average in this task (Isaksson et.al submitted manuscript).

It is rare to find a sex difference in a task that requires cognitive skills of high complexity, although performance may vary between individuals to some degree (Marchetti and Drent 2000; Griffin et al. 2015). However, in animals that have distinct differences between the sexes in terms of social hierarchy, territory size and dispersal distance, cognitive sex differences may occur (Jones et al. 2003; Perdue et al. 2011; Thys et al. 2017). In our observational spatial learning study undertaken in great tits (**paper V**), we found such differences.

Box 2

Setup for Motor Self-Regulation Studies

Before each experimental or training session, we moved the bird from its home cage to an experimental cage that I describe below (figure..). During both training and experimental sessions, the birds and the experimenter were in separate compartments of the room. In order to minimise disturbance of the birds there was a screen of dark smoke-coloured glass between the experimenter and the birds. As the experimenter's side of the screen was dark and the birds' side lit-up, it was possible to observe the birds without being seen by them.

The experimental cage that we used for all birds was a standard home cage (60 x 60 x 40 cm) that we had equipped with a special experimental box, measuring 36 x 21 x 25 cm. The box was made of wooden boards with an open side towards the bird's cage and transparent Plexiglas on the side facing the experimenter. Between the cage and the box, there was a sliding door that could be opened or closed by pulling a string. This made it possible either to keep the birds in the cage or to give them access to the box. At the bottom of the box, we had mounted a small rotatable platform that the experimenter could turn in either direction by pulling one of two strings. The birds had full view of the inside the box from the cage.

Figure B2.1: Experimental cage in cylinder task

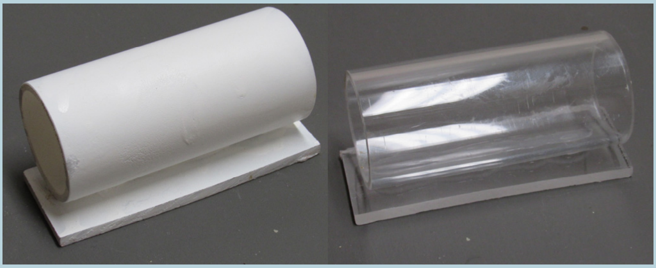

Figure B2.2: Opaque and transparent cylinder used in cylinder task

Therefore, in light of the results of our sex difference in observational learning study and that of recent motor self-regulation studies, it was worthwhile to investigate if there were any sex differences also in motor-self regulation ability. We did this in **paper VI**, where we carried our studies of cognitive sex differences in great tits one-step further. To do this we tested 33 great tits (17 males 16 females) in the transparent cylinder task. We also investigated if there is any sex related performance difference when the birds get prior experience with a plastic transparent cylinder compared to if they do not have such experience. Lack of experience with transparency is a potentially a confounding factor for this test. If the animal does not know how transparency works, it fails the cylinder task not because of lack of motor self-regulation but because it doesn't perceive the cylinder as a barrier. Thus, having previous experience has a potentially crucial effect on success in this task. Therefore, we had four main groups in our study; transparent cylinder-naïve and transparent cylinder-experienced males, and, transparent cylinder-naïve and transparent cylinder-experienced females. Cylinder-experienced birds was given the opportunity to explore a transparent cylinder in their home cage for three consecutive days prior to the experiment, whereas cylinder-naïve birds encountered a transparent cylinder for the first time during the experiment. Although there was no difference in the average over all motor self-regulation ability between male and female great tits, we found that male great tits that were cylinder-naïve learnt to master this task faster than their female counterparts. However, the female great tits' overall performance increased significantly and seemed to slightly surpass the performance of males if they had experienced the transparent tube prior to the experiment.

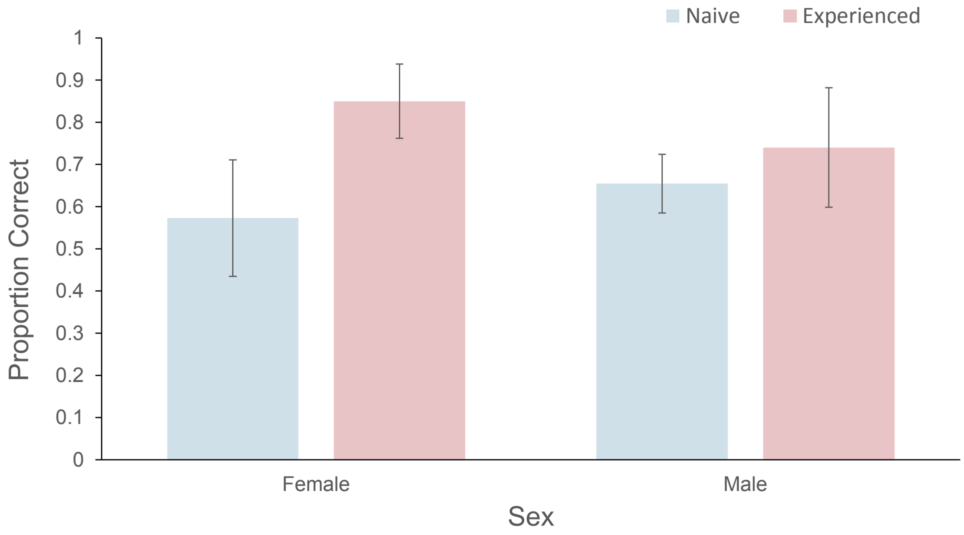

Figure 9.
Overall performance for experienced and naïve males and females exposed to the transparent cylinder task. The error bars are 95 % confidence intervals. Redrawn from **paper VI**

In great tits, exploratory behaviour is a consistent trait in males, yet it shows variety in females (Thys et al. 2017). We argue that sex difference in exploratory behaviour in great tits may have influenced the outcome of our study, as exploratory individuals are more likely to learn novel tasks faster. We also argue that sex differences in hierarchy could lead to learning differences between male and female great tits. Bold and dominant males are more likely to encounter novel objects and environments more frequently .While competing for food, male great tits are required to make quick decisions to gain an advantage, hence quick learning of novel tasks may be important. In females, however, quick learning may not be as important as the novel food sources are already dominated by males. Instead, female great tits may benefit from waiting, or following and observing males. In addition, we suggest that rank dependent motivational reasons could play a role in the outcome of our study. Females may be too alert due to presence of males in the laboratory and this alertness can be a restriction on their performance. However, after getting familiar with the cylinder, the effect of having dominant males in the same area may not be as strong.

Concluding Remarks

These studies suggest that the strategic dichotomy that is observed between food hoarding and non-hoarding parids, will result in differences in cognitive abilities. While marsh tits are good at specific tasks that are associated with a specialisation in food hoarding, the generalist great tit shows cognitive flexibility, which they use to exploit various food sources.

Regarding the first half of the dichotomy, the food hoarding experiments showed that marsh tits are successful in spatial memory tasks. Although they did not perform better than humans did, they remembered 40% of the locations of the caches. One reason for marsh tits' performing less accurately than humans could be memory interference due to repeated testing in the same environment. However, we eliminated this explanation in our memory interference test. The main objective of humans in this task was to retrieve the caches while making as few erroneous looks as possible. However, marsh tits may have looked for potential "extra" caches made by other conspecifics, which would be common under natural conditions. Such retrieval attempts would not be costly for the marsh tits but they would register as erroneous attempts and decrease the accuracy even if the marsh tits remembered all caches accurately. It is also possible that, marsh tits may still remember the locations of caches but may keep them for later.

Although marsh tits were successful in the food hoarding task, they were not as successful in the observational learning task as the great tits. We may ask, however, why they would have a need for this, as a specialised food hoarder with thousands of own caches they may not need another complex ability to gain a few extra caches. Remembered caches made by others would probably provide very little energy compared to what it can gain from making more own caches.

Turning to the other side of the dichotomy, where generalist great tits have to cope with the same harsh environmental conditions as the specialist food hoarders, such observational spatial memory ability could be very advantageous. Especially if the individual is a subordinate female that may be displaced from the food source by dominant males. Our results suggests that this sex difference in social rank is reflected in the cognitive abilities of male and female great tits. However, we cannot say whether males are actually worse than females, or whether they simply did not care. For example, young female chimpanzees spend more time watching their mothers to learn foraging skills than young male chimpanzees (Lonsdorf et al.

2004). According to Frans de Waal (2007) male chimpanzees are primarily concerned about “politics and sex” whereas the subordinate females pay more attention to learning of foraging skills.

A sex difference was present not only in the observational memorisation task but also in another cognitively complex task, the transparent cylinder task. As I have outlined before, this is a test for motor self-regulation ability which is the underlying mechanism for the ability of “self-control” (Beran 2015). The seemingly high ability of general motor self-regulation in great tits is not surprising considering, for example, the ability of great tits to open milk bottles (Fisher and Hinde 1949; Sherry and Galef 1984; Lefebvre and Boogert 2010), exploit hibernating bats as food, (Estók et al. 2010) and, their ability to use tools to forage in nature (Hoyo et al. 2007). However, I will not discuss this in this thesis as my focus is on the sex difference in learning of the specific motor self-regulation task. Even if we found no overall sex difference, males seemed to learn this faster than females. However, males did not perform significantly better after experiencing and possibly learning properties of cylinder and transparency, as females did. We argue that in addition to hierarchical differences, also sex dependent personality differences may play a part in learning in great tits.

In conclusion, the different sides of the winter foraging dichotomy in the *Paridae* family may select for different cognitive abilities to cope with similar environmental constraints. Cognitive differences are not only present between species but also between the sexes in great tits.

Acknowledgements

It isn't fair: the caterpillar does all the work, and the butterfly gets all the glory

George Carlin

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Box

You Are Welcome

You are all welcome for all the beer. I have spent hours making the pub list over the last few years, to make sure that the department of biology functions properly. I believe this has been appreciated (see figure below). I hope the next pub master can top this.

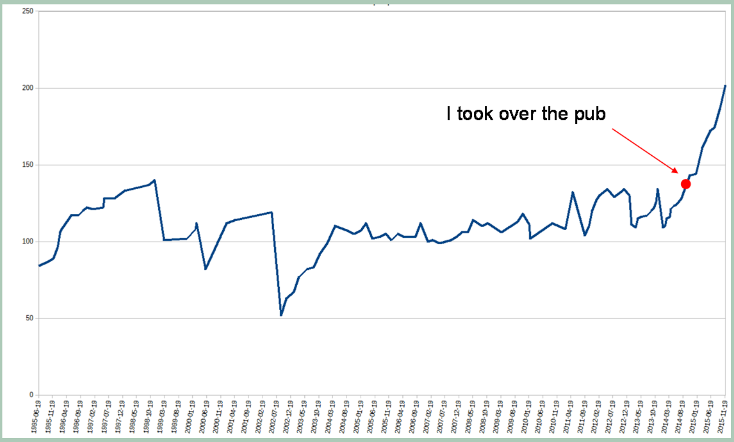


Figure:
A graph showing the number of people in the Pub Einar list over the years.

I know what you are all thinking – "but Utku, you also restarted the Friday football". You are welcome for that too. It was a great way to get out of the work for an hour in the middle of the day

References

Alatalo R V (1991) Hoarding sites in mixed flocks of Willow and Crested Tits. Ornis Scand 22:88–93.

Allen GL (2004) Human Spatial Memory. Lawrence Erlbaum Associates, Inc., Publishers, Mahwah, New Jersey

Andersson M, Krebs J (1978) On the evolution of hoarding behaviour. Anim Behav 26:707–711.

Aplin LM, Farine DR, Morand-Ferron J, et al (2015) Experimentally induced innovations lead to persistent culture via conformity in wild birds. Nature 518:538–541.

Astur RS, Ortiz ML, Sutherland RJ (1998) A characterization of performance by men and women in a virtual Morris water task: Behav Brain Res 93:185–190.

Auersperg a. MI, von Bayern a. MI, Weber S, et al (2014) Social transmission of tool use and tool manufacture in Goffin cockatoos (Cacatua goffini). Proc R Soc B Biol Sci 281:20140972–20140972.

Auersperg AMI, von Bayern AMP, Gajdon GK, et al (2011) Flexibility in problem solving and tool use of kea and new caledonian crows in a multi access box paradigm. PLoS One. 6:e20231

Baker MC, Stone E, Baker AEM, et al (1988) Evidence against observational-learning in storage and recovery of seeds by Black-capped Chicakdees. Auk 105:492–497.

Bednekoff PA, Balda RP (1996a) Social caching and observational spatial memory in pinyon jays. Behaviour 133:807–826.

Bednekoff PA, Balda RP (1996b) Observational Spatial Memory in Clark’s Nutcrackers and Mexican Jays. Anim Behav 52:833–839.

Beran MJ (2015) The comparative science of “self-control”: What are we talking about? Front Psychol 6:1–4.

Bradshaw JL, Gates EA (1978) Visual field differences in verbal tasks: Effects of task familiarity and sex of subject. Brain Lang 5:166–187.

Brodin A (2010) The history of scatter hoarding studies. Philos Trans R Soc Lond B Biol Sci 365:869–881.

Brodin A (2005) Mechanisms of cache retrieval in long-term hoarding birds. J Ethol 23:77–83.

Brodin A (1997) Why do hoarding birds gain fat in winter in the wrong way ? Suggestions from a dynamic model. Behav Ecol 11:27–39.

Brodin A (1992) Cache dispersion affects retrieval time in hoarding willow tits. Ornis Scand 23:7–12.

Brodin A (1993) Radio-ptilochronology: Tracing radioactively labelled food in feathers. Ornis Scand 24:167–173.

Brodin A, Ekman J (1994) Benefits of food hoarding. Nature 372:510.

Brodin A, Kunz C (1997) An Experimental Study of Cache Recovery By Hoarding Willow Tits After Different Retention Intervals. Behaviour 134:881–890.

Brodin A, Urhan AU (2014) Interspecific observational memory in a non-caching Parus species, the great tit Parus major. Behav Ecol Sociobiol 68:649–656.

Bugnyar T (2013) Social cognition in ravens. Comp Cogn Behav Rev 8:1–12.

Bugnyar T, Kotrschal K (2002) Observational learning and the raiding of food caches in ravens, Corvus corax: is it “tactical” deception? Anim Behav 64:185–195.

Bunch KG, Tomback DF (1986) Bolus recovery by gray jays: an experimental analysis. Anim Behav 34:754–762.

Burke A (2012) Spatial abilities, cognition and the pattern of Neanderthal and modern human dispersals. Quat Int 247:230–235.

Carere C, Van Oers K (2004) Shy and bold great tits (Parus major): Body temperature and breath rate in response to handling stress. Physiol Behav 82:905–912.

Cheng K, Graham P (2013) Spatial memory: Place learning, piloting, and route knowledge. Handb Spat Cogn 137–153.

Clayton NS (1993) Lateralization and unilateral transfer of spatial memory in marsh tits. J Comp Physiol A 171:799–806.

Clayton NS, Reboreda JC, Kacelnik A (1997) Seasonal changes of hippocampus volume in parasitic cowbirds. Behav Processes 41:237–243.

Cole EF, Cram DL, Quinn JL (2011) Individual variation in spontaneous problem-solving performance among wild great tits. Anim Behav 81:491–498.

Cook RG (1993) Symposium on Animal Cognition-The experimental analysis of cognition in animals. Psychol Sci 3:174–179.

Cowie RJ, Hinsley SA (1988) Feeding ecology of Great Tits (Parus major) and Blue Tits (Parus caeruleus), breeding in suburban gardens. JAnimEcol 57:611–626.

Cowie RJ, Krebs JR, Sherry DF (1981) Food storing by marsh tits. Anim Behav 29:1252–1259.

Cramp S, Perrins CM (1993) Handbook of the birds of Europe, the Middle East, and North Africa. The birds of the western Palearctic. Volume VII: Flycatchers to shrikes. Oxford University Press, Oxford, UK

Dabbs JM, Chang E-L, Strong R a, Milun R (1998) Spatial Ability, Navigation Strategy, and Geographic Knowledge Among Men and Women. Evol Hum Behav 19:89–98.

Dally JM, Clayton NS, Emery NJ (2006) The behaviour and evolution of cache protection and pilferage. Anim. Behav. 72:13–23.

Darwin C (1871) The Descent of Man. Penguin Books

De Waal FBM (2007) Chimpanzee politics : power and sex among apes. Johns Hopkins University Press

Diamond A (2013) Executive functions. Annu Rev Psychol 64:135–168.

Dukas R (1999) Costs of Memory: Ideas and Predictions. J Theor Biol 197:41–50.

Dukas R (1998) Constraints on information processing and their effects on behavior. Cognitive ecology (Dukas R, ed). Chicago: University of Chicago Press

Dunlap AS, Chen BB, Bednekoff PA, et al (2006) A state-dependent sex difference in spatial memory in pinyon jays, Gymnorhinus cyanocephalus: mated females forget as predicted by natural history. Anim Behav 72:401–411.

Ekman J (1989) Ecology of non-breeding social systems of Parus. Wilson Bull 101:263–288.

Ekman J (1987) Exposure and time use in willow tit flocks: the cost of subordination. Anim Behav 35:445–452.

Emery NJ (2006) Cognitive ornithology: the evolution of avian intelligence. Philos Trans R Soc Lond B Biol Sci 361:23–43.

Emery NJ, Clayton NS (2004) The Mentality of Crows: Convergent Evolution of Intelligence in Corvids and Apes. Science (80-) 306:1903–1907.

Emery NJ, Clayton NS (2005) Evolution of the avian brain and intelligence. Curr Biol 15:R946–R950.

Estók P, Zsebok S, Siemers BM (2010) Great tits search for, capture, kill and eat hibernating bats. Biol Lett 6:59–62.

Fisher J, Hinde RA (1949) The opening of milk bottles by birds. Br Birds 42:57.

Gaffan E a. (1992) Primacy, recency, and the variability of data in studies of animals' working memory. Anim. Learn. Behav. 20:240–252.

GALEF BG, LALAND KN (2005) Social Learning in Animals: Empirical Studies and Theoretical Models. Bioscience 55:489.

Garamszegi LZ, Eens M (2004) The evolution of hippocampus volume and brain size in relation to food hoarding in birds. Ecol Lett 7:1216–1224.

Gaulin SJ, FitzGerald RW, Wartell MS (1990) Sex differences in spatial ability and activity in two vole species (Microtus ochrogaster and M. pennsylvanicus). J Comp Psychol 104:88–93.

Gaulin SJC (1992) Evolution of sex difference in spatial ability. Am J Phys Anthropol 35:125–151.

Gaulin SJC, Fitzgerald RW (1989) Sexual selection for spatial-learning ability. Anim Behav 37:322–331.

Gentner D (2007) Spatial cognition in apes and humans. Trends Cogn. Sci. 11:192–194.

Gibb J (1954) Feeding ecology of tits, with notes on treecreeper and goldcrest. Ibis (Lond 1859) 96:513–543.

Giraldeau L-A, Valone TJ, Templeton JJ (2002) Potential disadvantages of using socially acquired information. Philos Trans R Soc B Biol Sci 357:1559–1566.

Gosler AG (1986) Pattern and process in the bill morphology of Great tits Parus major. Ibis (Lond 1859) 129:451–476.

Gosler AG, Clement PC-A (2007) Family *Paridae* (Tits and Chickadees). In: Handbook of the birds of the world, Picathartes to Tits and Chickadees. pp 662–731

Gould JL (2008) Cognition and behavioral ecology. Encycl Ecol 668–672.

Gresack JE, Frick KM (2003) Male mice exhibit better spatial working and reference memory than females in a water-escape radial arm maze task. Brain Res 982:98–107.

Griffin AS, Guillette LM, Healy SD (2015) Cognition and personality: An analysis of an emerging field. Trends Ecol. Evol. 30:207–214.

Guigueno MF, Snow D a, Macdougall-Shackleton S a, Sherry DF (2014) Female cowbirds have more accurate spatial memory than males. Biol Lett 10:20140026.

Güntürkün O, Bugnyar T (2016) Cognition without Cortex. Trends Cogn Sci 20:291–303.

Haftorn S (1959) The proportion of spruce seeds removed bythe tits in a Norwegian spruce forest in 1954–55. Kgl Nor Videnskaapers Selsk Forh 32:121–125.

Halpern DF (2013) Sex Differences in Cognitive Abilities, 4th Editio. Psychology Press

Hampton RR, Shettleworth SJ, Westwood RP (1998) Proactive interference, recency, and associative strength: Comparisons of black-capped chickadees and dark-eyed juncos. Anim. Learn. Behav. 26:475–485.

Harvey PH, Greenwood PJ, Perrins CM (1979) Breeding Area Fidelity of Great Tits (Parus major). J Anim Ecol 48:305.

Haun DBM, Jordan FM, Vallortigara G, Clayton NS (2011) Origins of Spatial, Temporal, and Numerical Cognition: Insights from Comparative Psychology. In: Space, Time and Number in the Brain. Elsevier Inc., pp 191–206

Hausmann M, Schoofs D, Rosenthal HES, Jordan K (2009) Interactive effects of sex hormones and gender stereotypes on cognitive sex differences-A psychobiosocial approach. Psychoneuroendocrinology 34:389–401.

Healy S, Suhonen J (1996) Memory for locations of stored food in willow tits and marsh tits. Behaviour 133:71–80.

Healy SD, Krebs JR (1992) Delayed-matching-to-sample by marsh tits and great tits. Q J Exp Psychol Sect B Comp Physiol Psychol 45:33–47.

Heinrich B, Pepper JW (1998) Influence of competitors on caching behavior in the common raven, Corvus corax. Anim Behav 56:1083–1090.

Henson RN (1998) Short-term memory for serial order: the Start-End Model. Cogn Psychol 36:73–137.

Herculano-Houzel S (2017) Numbers of neurons as biological correlates of cognitive capability. Curr Opin Behav Sci 16:1–7.

Herz R, Zanette L, Sherry DF (1994) Spatial cues for cache retrieval by black-capped chickadees. Anim Behav 48:343–351.

Heyes C, Galef BJ (1996) Social learning and the roots of culture. San Diego: Academic Press

Hilton S, Krebs J (1990) Spatial memory of four species of Parus: performance in an open-field analogue of a radial maze. Q J Exp Psychol Sect B Comp Physiol Psychol 42:345–368.

Hitchcock CL, Sherry DF (1990) Long-term memory for cache sites in the black-capped chickadee. Anim. Behav. 40:701–712.

Hitchcock CLC, Sherry DF (1995) Cache Pilfering and Its Prevention in Pairs of Black-Capped Chickadees. J Avian Biol 26:187–192.

Hoyo J Del, Elliott A, Christie D (2007) Handbook of the birds of the world. Volume 12. Picathartes to tits and chickadees, Lynx Edici. Barcelona

Isaksson E, Urhan AU, Brodin A (2017) High level of self-control ability in a small passerine bird. Manuscript submitted for publication.

Jitsumori M, Wright AA, Cook RG (1988) Long-term proactive interference and novelty enhancement effect in monkey list memory. J Exp Psychol Anim Behav Process 14:146–154.

Jones CM, Braithwaite VA, Healy SD (2003) The evolution of sex differences in spatial ability. Behav Neurosci 117:403–411.

Kabadayi C, Osvath M (2017) Ravens parallel great apes in flexible planning for tool-use and bartering. Science (80-) 357:202–204.

Kabadayi C, Taylor LA, Bayern AMP von, Osvath M (2016) Ravens, New Caledonian crows and jackdaws parallel great apes in motor self-regulation despite smaller brains. RSoc.open sci 3:160104.

Keppel G, Underwood BJ (1962) Proactive inhibition in short-term retention of single items. J Verbal Learning Verbal Behav 1:153–161.

King JR, Muddeman JL (1995) Ageing and sexing Marsh Tits Parus palustris. Ringing Migr 16:172–177.

Klatzky RL (1998) Allocentric and egocentric spatial representations: Definitions, distinctions, and interconnections. 1404:1–17.

Krebs JR, Clayton NS, Healy SD, et al (1996) The ecology of the avian brain: food-storing memory and the hippocampus. Ibis (Lond 1859) 138:34–46.

Krebs JR, MacRoberts MH, Cullen JM (1972) Flocking and feeding in the great tit parus major–an experimental study. Ibis (Lond 1859) 114:507–530.

Krebs JR, Sherry DF, Healy SD, et al (1989) Hippocampal specialization of food-storing birds. Proc Natl Acad Sci U S A 86:1388–92.

Krushinskaya N (1966) Some complex forms of feeding behaviour of nutcracker Nucifraga caryocatactes, after removal of old cortex. Zh Evol Biokhim Fiziol 11:563–568.

Laland KN (1996) Is social learning always locally adaptive? Anim Behav 52:637–640.

Laland KN (2004) Social learning strategies. Anim Learn Behav 32:4–14.

Lefebvre L, Boogert NJ (2010) Avian Social Learning. Encycl Anim Behav 1:124–130.

Lewis JL, Kamil AC (2006) Interference effects in the memory for serially presented locations in Clark’s nutcrackers, Nucifraga columbiana. J Exp Psychol Anim Behav Process 32:407–18.

Lonsdorf E V, Eberly LE, Pusey AE (2004) Sex differences in learning in chimpanzees. Nature 428:715–716.

Lucas JR, Brodin A, de Kort SR, Clayton NS (2004) Does hippocampal size correlate with the degree of caching specialization? Proc Biol Sci 271:2423–9.

Luria A (1966) The Higher Cortical Functions in Man. Basic Books, New York

MacLean EL, Hare B, Nunn CL, et al (2014) The evolution of self-control. Proc Natl Acad Sci U S A 111:E2140-8.

MacLean EL, Matthews LJ, Hare B a, et al (2012) How does cognition evolve? Phylogenetic comparative psychology. Anim Cogn 15:223–238.

Macphail EEM (2002) The role of the avian hippocampus in spatial memory. Psicológica Rev Metodol y Psicol 23:93–108.

Marchetti C, Drent PJ (2000) Individual differences in the use of social information in foraging by captive great tits. Anim Behav 60:131–140.

McBurney DH, Gaulin SJ., Devineni T, Adams C (1997) Superior spatial memory of women: Stronger evidence for the gathering hypothesis. Evol. Hum. Behav. 18:165–174.

McNamara JM, Houston AI, Krebs JR (1990) Why hoard? The economics of food storing in tits, Parus spp. Behav Ecol 1:12–23.

Mendl M, Laughlin K, Hitchcock D (1997) Pigs in space: spatial memory and its susceptibility to interference. Anim Behav 54:1491–1508.

Miller DI, Halpern DF (2014) The new science of cognitive sex differences. Trends Cogn. Sci. 18:37–45.

Mishima N, Higashitani F, Teraoka K, Yoshioka R (1986) Sex differences in appetitive learning of mice. Physiol Behav 37:263–268.

Moffat SD, Hampson E, Hatzipantelis M (1998) Navigation in a “Virtual” Maze: Sex Differences and Correlation With Psychometric Measures of Spatial Ability in Humans. Evol Hum Behav 19:73–87.

Morley A (1950) The formation and persistence of pairs in the Marsh Tit. Br Birds 43:387–393.

Morley A (1953) Field observations on the biology of the Marsh Tit. Br Birds 46:233–238.

Olkowicz S, Kocourek M, Lučan RK, et al (2016) Birds have primate-like numbers of neurons in the forebrain. Proc Natl Acad Sci 113:7255–7260.3

Olmstead MC, Kuhlmeier VA (2015) Comparative cognition. Cambridge University Press

Olson DJ, Kamil AC, Balda RP, Nims PJ (1995) Performance of four seed-caching corvid species in operant tests of nonspatial and spatial memory. J Comp Psychol 109:173–181.

Olton D, Paras B (1979) Spatial memory and hippocampal function. Neuropsychologia 17:669–682.

Olton DS, Samuelson RJ (1976) Remembrance of places passed: Spatial memory in rats. J. Exp. Psychol. Anim. Behav. Process. 2:97–116.

Osvath M, Kabadayi C, Jacobs I (2014) Independent Evolution of Similar Complex Cognitive Skills : The Importance of Embodied Degrees of Freedom. Anim Behav Cogn 1:249–264.

Osvath M, Osvath H (2008) Chimpanzee (Pan troglodytes) and orangutan (Pongo abelii) forethought: Self-control and pre-experience in the face of future tool use. Anim Cogn 11:661–674.

Ottvall R, Edenius L, Elmberg J, Engström H (2008) Populationstrender för fågelarter som häckar i Sverige. Stockholm

Pearce JM (2013) Animal learning and cognition: an introduction. Psychology Press

Perdue BM, Snyder RJ, Zhihe Z, et al (2011) Sex differences in spatial ability: a test of the range size hypothesis in the order Carnivora. Biol Lett 7:380–3.

Petersen K, Sherry DF (1996) No sex difference occurs in hippocampus, food-storing, or memory for food caches in black-capped chickadees. Behav Brain Res 79:15–22.

Pravosudov V V., Lucas JR (2001) A dynamic model of short-term energy management in small food-caching and non-caching birds. Behav Ecol 12:207–218.

Ricklefs RE (2004) THE COGNITIVE FACE OF AVIAN LIFE HISTORIES: The 2003 Margaret Morse Nice Lecture. Wilson Bull. 116:119–133.

Roitblat HL, Harley HE (1988) Spatial delayed matching-to-sample performance by rats: Learning, memory, and proactive interference. J Exp Psychol Anim Behav Process 14:71–82.

Sasva L, Sasvári L, Hegyi Z (1998) How mixed-species foraging flocks develop in response to benefits from observational learning. Anim Behav 55:1461–1469.

Sasvári L (1992) Great tits benefit from feeding in mixed-species flocks: a field experiment. Anim Behav 43:289–296.

Sasvári L (1979) Observational learning in great, blue and marsh tits. Anim Behav 27:767–771.

Sasväri L (1985) Different observational learning capacity in juvenile and adult individuals of congeneric bird species. Z Tierpsychol 69:293–304.

Scheid C, Bugnyar T (2008) Short-term observational spatial memory in Jackdaws (Corvus monedula) and Ravens (Corvus corax). Anim Cogn 11:691–698.

Sherry DF (2006) Neuroecology. In: Annual Review of Psychology. pp 167–197

Sherry DF (1985) Food Storage by Birds and Mammals. Adv Study Behav 15:153–188.

Sherry DF (1984) Food storage by black-capped chickadees: Memory for the location and contents of caches. Anim. Behav. 32:451–464.

Sherry DF, Galef BG (1984) Cultural transmission without imitation: Milk bottle opening by birds. Anim Behav 32:937–938.

Sherry DF, Krebs JR, Cowie RJ (1981) Memory for the location of stored food in marsh tits. Anim Behav 29:1260–1266.

Sherry DF, Vaccarino AL (1989) Hippocampus and memory for food caches in black-capped chickadees. Behav Neurosci 103:308–318.

Sherry DFDF, Vaccarino ALAL, Buckenham K, Herz RSRS (1989) The Hippocampal Complex of Food-Storing Birds. Brain Behav Evol 34:308–317.

Shettleworth SJ (1998) Cognition, evolution, and behavior. Oxford University Press, Oxford, UK

Shettleworth SJ (1990) Spatial Memory in Food-Storing Birds. Philos. Trans. R. Soc. B Biol. Sci. 329:143–151.

Shettleworth SJ (2001) Animal cognition and animal behaviour. Anim Behav 61:277–286.

Shettleworth SJ (2003) Memory and hippocampal specialization in food-storing birds: Challenges for research on comparative cognition. In: Brain, Behavior and Evolution. pp 108–116

Shettleworth SJ, Krebs JR (1982) How marsh tits find their hoards: the roles of site preference and spatial memory. J Exp Psychol Anim Behav Process 8:354–375.

Shettleworth SJ, Krebs JR (1986) Stored and encountered seeds: a comparison of two spatial memory tasks in marsh tits and chickadees. J Exp Psychol Anim Behav Process 12:248–257.

Shine R (1989) Ecological Causes for the Evolution of Sexual Dimorphism: A Review of the Evidence. Q Rev Biol 64:419–461.

Slagsvold T, Wiebe KL (2011) Social learning in birds and its role in shaping a foraging niche. Philos Trans R Soc Lond B Biol Sci 366:969–77.

Smith CC, Reichman OJ (1984) The Evolution of Food Caching by Birds and Mammals. Annu Rev Ecol Syst 15:329–351.

Smulders T V (1998) A game theoretical model of the evolution of food hoarding: applications to the *Paridae*. Am Nat 151:356–66.

Snow D, Perrins C, Gillmor R (1998) The birds of the Western Palearctic Vol.2, Concise Ed. Oxford University Press, Oxford, UK

Squire LR (1992) Memory and the hippocampus: a synthesis from findings with rats, monkeys, and humans. Psychol Rev 99:195–231.

Stevens TA, Krebs JR (1986) Retrieval of stored seeds by marsh tits Parus palustris in the field. Ibis (Lond 1859) 128:513–525.

Swanberg PO (1951) Food storage, territory and song in the thick- billed nutcracker. In: Hörstadius S (ed). Proc 10th Int Ornithol Congr 1950, Uppsala Almqvist Wiksell, Uppsala 545–554.

Thornton A, Lukas D (2012) Individual variation in cognitive performance: developmental and evolutionary perspectives. Philos Trans R Soc B Biol Sci 367:2773–2783.

Thys B, Pinxten R, Raap T, et al (2017) The Female Perspective of Personality in a Wild Songbird: Repeatable Aggressiveness Relates to Exploration Behaviour. Sci Rep 7:7656.

Tomback D (1980) How nutcrackers find their seed stores. Condor 82:10–19.

Tschirren B, Fitze PS, Richner H (2003) Sexual dimorphism in susceptibility to parasites and cell-mediated immunity in great tit nestlings. J Anim Ecol 72:839–845.

Ulfstrand S (1962) On the nonbreeding ecology and migratory movements of the great tit (Parus major) and the blue tit (Parus caeruleus) in southern Sweden: with notes on.

Vander Wall SB (1990) Food Hoarding in Animals. University of Chicago Press

Vander Wall SB (1982) An experimental analysis of cache recovery in Clark's nutcracker. Anim. Behav. 30:84–94.

Vander Wall SB, Jenkins SH (2003) Reciprocal pilferage and the evolution of food-hoarding behavior. Behav Ecol 14:656–667.

Voyer D, Voyer S, Bryden MP, et al (1995) Magnitude of Sex Differences in Spatial Abilities: A Meta-Analysis and Consideration of Critical Variables. Psychol Bull 117:250–270.

Wasserman EA, Zentall TR (2012) Comparative Cognition: Experimental Explorations of Animal Intelligence. Oxford University Press, Oxford, UK

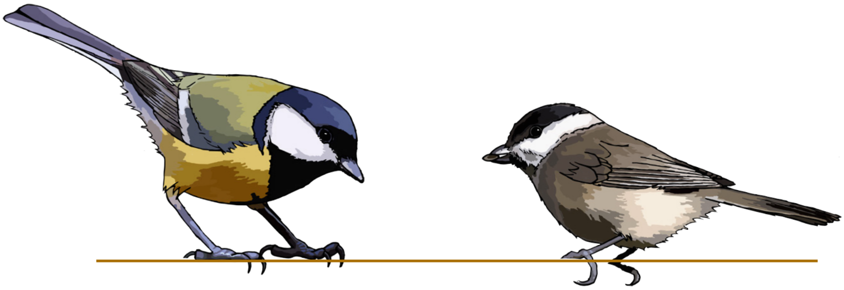
Watanabe S, Clayton NS (2007) Observational visuospatial encoding of the cache locations of others by western scrub-jays (Aphelocoma californica). J Ethol 25:271–279.

Weiss EM, Kemmler G, Deisenhammer EA, et al (2003) Sex differences in cognitive functions. Pers Individ Dif 35:863–875.

Williams CL, Meck WH (1991) The organizational effects of gonadal steroids on sexually dimorphic spatial ability. Psychoneuroendocrinology 16:155–176.

Wright AA, Urcuioli PJ, Sands SF (1986) Proactive Interference in Animal Memory. In: In D.F Kendrick, M. Rilling & R. Denny (Eds) Theories of Animal Memory. Erlbaum, Hillside, NJ, pp 101–125

Wynn T (2002) Archaeology and cognitive evolution. Behav Brain Sci 25:338–389.



Comparative studies of cognitive abilities in the *Paridae*

I. Brodin, A., & Urhan, A. U. (2013). An evaluation of memory accuracy in food hoarding marsh tits *Poecile palustris* - how accurate are they compared to humans? Behavioural Processes, 97, 25–32.

II. Brodin, A., & Urhan, A. U. (2014). Interspecific observational memory in a non-caching Parus species, the great tit *Parus major*. Behavioral Ecology and Sociobiology, 68(4), 649–656.

III. Brodin, A., & Urhan, A. U. (2015). Sex differences in learning ability in a common songbird, the great tit — females are better observational learners than males. Behavioral Ecology and Sociobiology, 69(2), 237–241.

IV. Urhan, A. U., & Brodin, A. (2015). No evidence for memory interference across sessions in food hoarding marsh tits *Poecile palustris* under laboratory conditions. Animal Cognition, 18(3), 649–656.

V. Urhan, A. U., Emilsson, E., & Brodin, A. (2017). Evidence against observational spatial memory for cache locations of conspecifics in marsh tits *Poecile palustris*. Behavioral Ecology and Sociobiology, 71(2), 34.

VI. Urhan, A. U., Isaksson, E., & Brodin., A. (2017) Sex difference in learning rate of motor self-regulation in great tits, *Parus major* (Manuscript)

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