Norwegian University of Life Sciences

Master's Thesis 2020 60 ECTS
Faculty of Environmental Science and Natural Resource Management

Cafeteria experiment: Acorn preference of the Eurasian Jay (*Garrulus glandarius*)

Andrea Helene Stensvold
Master of Science in General Ecology

Preface

This thesis concludes my master thesis in General Ecology at The Norwegian University of Life Sciences (NMBU). I would firstly, thank my supervisor Ronny Steen for all the constructive feedback and help throughout the entire process from finding a successful project to finalizing the thesis. I would then like to thank Arnkjell Johansen for helping me build bird boxes, even though the first project about jackdaws (*Corvus monedula*) fell through. I would also like to thank Mathias Jerpseth, for helping sorting acorns in the first experiment. Further, I would like to thank Mikaela Olsen for feedback on my text and being a good friend and study partner through my entire study. Finally, I would like to thank my friends Julianne Sundklakk and Solveig Strålberg, and my family for always being positive and giving me great support.

Abstract

Food hoarding is a strategy that is beneficial during food scarcity and improves the chance of survival. Seasonal fluctuations in food availability is common, and during the winter there are less food available. Eurasian Jays (*Garrulus glandarius*) is a common food hoarder and collects food during late summer and fall to survive during food scarcity in the winter. Jays' main food storage is the Quercus acorns, and these are only available for a short period. It is important to cache many, but also vital acorns that can withstand a long storing period.

The main objective of this study was to see if the Eurasian jays had a preference in terms of quality of the acorns when hoarding. When collecting acorns on the ground the jays should select freshly fallen acorns to avoid mold or damages caused by ground dwelling small mammals. Further, the jays should omit acorn with holes as they can be infected by weevils (*Curculio spp.* and *Conotrachelus spp*). In this study I would like to see if the jays were selective when collecting acorns for storage. Old acorns could be moldy, acorns infected by weevils or damaged by rodents will have a higher chance of getting spoiled during storage. Thus, the jays should benefit more from collecting sound acorns.

In this study I found that jays make deliberate decisions when there are many acorns available. They preferred acorns of higher quality (i.e. intact and fresh acorns). When there are less preferable acorns available, the jays choose the less favorable acorns, such as damaged and acorns with holes.

Table of contents

Introduction

Food hoarding has developed separately in many different groups of animals, from birds and mammals to invertebrates, and has been documented by humans for a long time (Brodin, 2010; Roberts, 1979). Food hoarders cache food for later consumption and it can be defined as "the handling of food to conserve it for future use" (Vander Wall, 1990). There are many strategies and reasons for a specific animal to choose to cache food, and many have evolved their own strategies and techniques to maximize the success of the caching. The forager, the environment in which to forage, and the type of food that is cached is a complex interaction.

Optimal foraging strategy is a theory that assumes that natural selection favors the strategy that maximizes the forager's fitness (McNamara & Houston, 1985). The fitness is maximized if the energetic gain is bigger than the energetic restrain (Stephens & Krebs, 1986). There are two main strategies for food caching: scatter hoarding and larder hoarding. A larder hoarder stores all their food in one place. An example of a larder hoarder is the honeybee (*Apis mellifera*), which store all their food in the beehive (Free & Williams, 1972). A scatter hoarder scatters their food in different places. One example of a scatter hoarder is the fox squirrel (*Sciurus niger*) which caches black walnuts (*Julgans nigra*) and store them on separate locations (Stapanian & Smith, 1978).

An important aspect of hoarding is the handling of the food. Handling can prevent other animals from consuming it by hiding it or making the food less available for bacterial attack and decomposition. Handling of the food includes preparation, transportation, placement and concealment (Vander Wall, 1990). Travel time to and from the food source, how much to carry at a time, and where and how to bury the food is taken into consideration when storing food. However, when the food is stored, it can either spoil or improve (ripen) (Gendron & Reichman, 1995). The more food that is stored together, the higher the chances are that it will be found by insects (Wilson & Janzen, 1972).

Whether animals decide to store food for a long or short period of time, stored food sources can be the only chance of survival when less food is available. When food sources are scarce, food hoarders can turn to their caches, while non hoarding animals may be forced to migrate to locations where food is available, hibernate or decrease in body mass (Vander Wall, 1990). Fluctuations in food availability may occur under unpredictable environmental conditions, or predictably during seasonal changes. Birds that inhabit the north temperate latitudes are often exposed to seasonal resource availability fluctuations (Roberts, 1979). Some of the birds that live in these areas migrate south, but many birds will choose to stay put. Therefore, many resident birds cache food to make sure they can obtain food during the winter when food sources are less abundant (Roberts, 1979; Vander Wall, 1990). One of these resident birds in Norway are the Eurasian Jay (*Garullus glandarius*).

Jays experience seasonal fluctuations in food availability, since their largest food supply comes from trees (e.g. oaks (Quercus spp.)), which produce all their seeds in late summer and early fall, and with irregular amounts of seeds every year (Selås, 2017). It is therefore important for the jays to gather enough acorns to feed them throughout the winter, when other food sources are scarce or when large parts of the land are covered in snow. It is also important to hide their food sources where they are less likely to be found by their peers, or by other animals which feed on acorns, such as mice (*Muridae*), deer (*Cervidae*), squirrels (*Sciuridae*) and other birds (Vander Wall, 1990).

The dispersal of oak by Eurasian Jays is well known (Bossema, 1979). A study done in Hainhault Forest in Essex England showed that thirty-five Eurasian jays stored nearly 200 000 acorns during the fall of 1951 (Chettleburgh, 1952). Studies show that the dispersal and burial of acorns benefits the oaks, and that the oak community is shaped by these birds (Bossema, 1979; Gómez, 2003; Vander Wall, 2001). Jays store acorns on separate locations, also known as scatter hoarding (Smith & Reichman, 1984). Not all the acorns are found and eaten, and therefore some acorns are left to grow up to become oaks. Jays cache food during the fall months and will eat from their storage throughout the winter months (Bossema, 1979). This can also benefit their young, when other food sources are limited (Bossema, 1979).

The jays should also make decisions on which acorns to store, and which should be consumed right away. Storing food is riskier than eating it immediately, as cached food may be spoiled, forgotten or taken by other animals (Davies et al., 2012). The jays store acorns, but acorns differ, as some acorns are parasitized by weevils (*Curculio spp.* and *Conotrachelus spp.),* some are infected with fungi (*Ciboria batschiana*), and some are partially consumed by rodents (Schroder, 2002; Steele et al., 1996; Vander Wall, 2001). The jays therefore need to make decisions on how much time to spend on gathering, carrying and burying, compared to the value of each acorn. The successful retrieval of acorns should also be taken into consideration when collecting and hiding acorns.

Crows are very intelligent, and have highly developed cognitive abilities (Emery & Clayton, 2004; Grodzinski & Clayton, 2010). For food storing animals, especially, it is important to remember what they have stored, when they have stored it and where they have stored it. Scrub jays (*Aphelocoma californica*) were capable to find the more perishable food first, such as worms. After a while, they stopped locating this type of food, knowing that it might have spoiled (Clayton & Dickinson, 1998). The same cognitive abilities are important for the Eurasian jays when storing acorns during autumn, as they might ripen or spoil at different times dependent on the quality of the acorns that are stored. It is therefore interesting and important to study jays and their choices in the wild to see if the jays are able to plan for the future.

Aim of this study

The main objective of this study was to see if the Eurasian jays were picking the "right" acorn, in terms of quality. Acorns are green before they ripen, as they ripe they turn yellow and finally brown, when ripened the acorns fall (Janick & Paull, 2008). Jays are often seen eating acorns directly from the tree or at the ground (Madge & Burn, 1994), although when collecting acorns on the ground the jays should select freshly fallen acorns to avoid mold or damages caused by ground dwelling small mammals. Further, the jays should omit acorn with holes as they can be infected by weevils. In this study I would like to see if the jays were selective when collecting acorns for food storage. Old acorns that could be moldy, acorns infected by weevils or damaged by rodents will have a higher chance of getting spoiled during storage, and the jays should therefore benefit more from collecting sound acorns. It would be more beneficial to use time and effort storing acorns that have a higher probability having an energetic reward (Davies et al., 2012).

Hypotheses

H_0 – no preference for any of the different acorn qualities.

H_1 – preference for light brown and fresh acorns compared to dark brown acorns. I expect this outcome because light brown acorns are more likely to be freshly fallen to the ground and may last longer during storage.

H_2 – preference for intact acorns compared to damaged acorns (e.g. eaten by rodents) and acorns with holes (i.e. infected by weevils). I expect this outcome because intact acorns will have a high chance of survival until retrieval, and intact acorns will offer more food than damaged or partial eaten acorns.

Methods

I will firstly present the study species, before looking at the study location. Further, I will explain the study setup. Next I will explain the execution of the two different cafeteria experiments that was executed. Lastly, I will go through the data analysis for the two experiments separately.

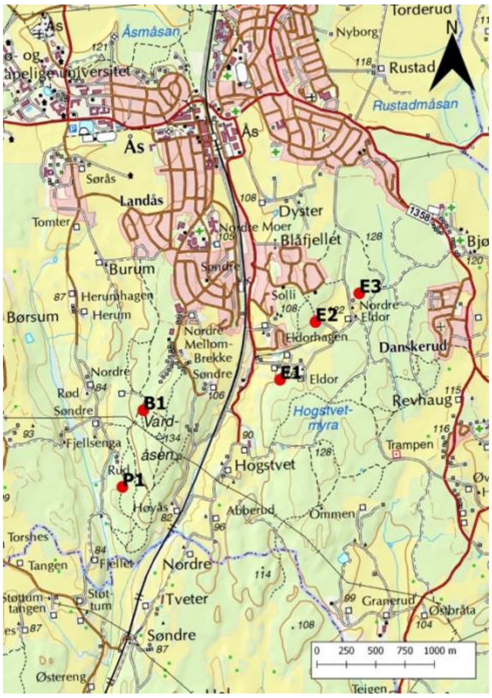
Study species

Eurasian Jay is a woodland species in the corvid family. Jays are common in all of Eurasia, and is a regular breeder in coniferous and mixed forests from southern Norway to Northern Norway (Haftorn, 1971). The Eurasian jay is the main dispersers of oak seeds in Western Europe (Bossema, 1979), and it is the main dispersers of the two native oak species in Norway; the common oak (*Quercus robur*) and sessile oak (*Quercus petraea*).

The Jay is an omnivore, and the diet changes with the seasons. During the summertime, the jays will eat a variety of foods ranging from fruits and nuts to insects, eggs and hatchlings. During the wintertime, the diet consists mostly of acorns collected during the fall. From August to November, the Eurasian jay collect many acorns for eating and storing (Haftorn, 1971). Acorns are either collected directly from the tree or from the ground. The jay carries several acorns at a time, they are carried in the oesophagus and the throat, and the last acorn is often carried in the bill (Bossema, 1979). The more acorns that is carried at once, the longer is the transportation distance. The acorns are stored on separate locations, preferably under a thin layer of dead leaves (Chettleburgh, 1952). The acorns are later retrieved as winter food or food for fledglings in the spring (Bossema, 1979).

Study location

The study was situated in the forests of Ås municipality, in Viken county, in Southeast Norway. The study area consisted of five different areas: P1, B1, E1, E2 and E3 (*figure 1*). P1 was in a mixed forest. B1 was in a mostly deciduous forest, with elements of coniferous trees. E1 was in a mostly coniferous forest, with elements of deciduous trees. E2 and E3 was both located in deciduous forests.



Coordinates for each study location:

P1 – 59.636771°N, 010.779210°E

B1 – 59.642575°N, 010.782689°E

E1 – 59.644623°N, 010.803448°E

E2 – 59.648951°N, 010.809033°E

E3 – 59.651042°N, 010.815764°E

Figure 1 Map of study area in Ås, Viken (left), with coordinates for each study site (right).

Study setup

A feeding station was provided in each location on September 2nd, 2019, with bird feeders and food on the ground. The feeding trays were placed on October 5th. Each station consisted of separate plastic boxes drilled to a wooden plank to separate the different types of acorns used in the study (*figure 2*). A camera was mounted approximately forty centimeters above the boxes. A bird feeder was placed near each of the feeding stations.

Each station had a time-lapse camera, Brinno TLC200 PRO (Brinno Inc., Taiwan) mounted, and the cameras were protected with a weather-resistant housing (Brinno ATH120). Four AA nickel metal hydride (NiMH) 2450mAh batteries (Fujitsu, Ltd., Tokyo, Japan) were used in each camera. The footage was stored onto SanDisk 32GB Class 4 SDHC Memory Cards (Sandisk Corp., USA). New batteries and new SD cards were used each trial. The time interval for the cameras were set to 1 frame per second, giving us one image every second. From the images, the camera produced an AVI (Audio Video Interleaved). VLC media player (http://www.videolan.org/vlc/) were used to review the footage (Steen et al., 2017).

Figure 2 The study setup (A), and screenshots of the study setup with acorns for experiment one (B), and experiment two (C). B: light brown acorns (left) and dark brown acorns (right). C: acorns with holes (left), damaged (middle) and intact (left).

Execution

Food was contributed on a regular basis beginning on the 2nd of September 2019 to ensure that the birds would visit the feedings stations during the study. The feeding stations were filled with peanuts and the bird feeders with sunflowers seeds. The bird feeders were filled with sunflowers throughout the entire study. The study concluded October 29th.

Table 1 Number of trials per location for cafeteria experiment one and two.

Trials per study location					
	B1	E1	E2	E3	P1
Experiment one	6	4	9	9	9
Experiment two	5	5	4	5	5

Cafeteria experiment one

Acorns were collected in September and stored inside for a few weeks prior to the study session, and were collected in Vestfold and Telemark county, in Færder municipality. Half of the acorns got three drilled holes (3mm) to mimic damage done by insects (Jones, 1959). The study took place in October, the time when jays are most active collecting acorns (Bossema, 1979). Five of the acorns with holes and five of the intact acorns were put in their separate boxes on each site each day. The trials ended when the sun went down or when there were no acorns left. On some days, more than one trial was conducted, one in the morning and one in the afternoon. If there were any acorns left, they were removed before a new trial.

Although, after the implementation of the cafeteria experiment, I realized when inspecting the video footage that the drilled acorns were much lighter in color than the intact acorns, further the intact acorns were also a bit creased. Hence, by storing the acorns for several weeks it altered the quality of the acorns, and not intended the acorns with holes had a fresher brown look. I therefore got the video footage processed by a "blind" observer being unfamiliar with the aim of the study. The observer was given 26 snapshots from the footage and asked to review the color of the contents. Two possible outcomes were given: light- and dark brown. As expected almost all the acorns with holes were classified as light, and all the sound acorns were classified as dark. In one snapshot (location E3, ninth trial) all the acorns were classified as light.

Cafeteria experiment two

Based upon the experience from experiment one, I decided to improve the methodological design of the study. To avoid altering the quality of the acorns by storing, I instead used acorns collected the day before each trial. For this experiment I collected acorns from three different oak trees in Ås. For the given setup I expanded the acorn selection and offered the Eurasian Jays with: i) intact acorns, ii) with holes (mimic infection by weevils) and iii) naturally damaged (e.g. inflicted by rodents or having similar damage). To mimic holes caused by insects, four holes (3mm) were drilled in selected acorns. With this setup intact acorns and acorns with holes had the same quality and only differed in terms of the holes.

The study was conducted after cafeteria experiment one, in late October/early November. Five of each acorn category were put in the boxes on each site (*figure 1*). The trials ended when the sun went down, or when no acorns were left in the boxes. There was only one trial per day per locality, and they were executed as consecutive as possible.

Data analysis

All statistical analysis was conducted using R studio version 1.2.1335 (R Core Team 2019). I created models using generalized linear mixed effect models (GLMM, package "LME4") with location as a random effect (5 localities). I fitted the models using a binomial distribution, since every observation was based on the jay choosing a light acorn or not (experiment one) or an intact acorn or not (experiment two). In experiment two, acorns with holes and damaged were pooled to enable a binomial outcome of the response (i.e. intact vs. non-intact acorn).

Experiment one

The response variable (y) was binomial (two outcomes): light vs. dark. The explanatory variables were the number of dark and light acorns available in the boxes and the interactions between them. At the initiation of the experiment the number of acorns were the same in both boxes, although the numbers decreased during the day as the jays collected acorns. Hence, by including number of acorns in each box in the statistical test I could control if the abundance of the different acorns influenced their choice.

Experiment two

The response variable (y) was binomial (two outcomes): intact vs. non-intact (with holes and damaged; pooled). The explanatory variables were the number of intact acorns, acorns with holes and damaged acorns present in the boxes. Despite reducing the response variable into a binomial outcome, I could test if the amount of each of the three acorn categories had an effect on the jay's choice. At the initiation of the experiment the number of acorns were the same in all three boxes, although the numbers decreased during the day as the jays collected acorns. Hence, by including number of acorns present in each box in the statistical test I could control if the abundance of the different acorns influenced their choice.

To test which models were the best, I conducted an ANOVA test with the "AICcmodavg" package in R. The best models were chosen based on which had the lowest AICc or was the most parsimonious model (Burnham et al., 2011). The best models were then used to create predictions and bootstrap (package "lme4") was used to generate 95% confidence intervals.

Results

I will firstly present cafeteria experiment one, starting by showing the acorn removal done by all the animals. I will then present the different models that was tested for cafeteria experiment one, before showing the parameter estimates from the best model. Then, I will show the predictions that were made from the parameter estimates. I will then repeat the same setup, but this time for the cafeteria experiment two. The predictions for experiment two are presented in a 2D and a 3D graph.

Acorn removal for experiment one – light vs. dark brown acorns

Overall, light acorns were, to a large extent, chosen first. As the number of light acorns in the overall supply decreased, more dark acorns were chosen (*figure 3*). In total, 325 acorns were removed: from which the Eurasian jay collected 309 acorns, Eurasian nuthatches (*Sitta europea*) 2, great tits (*Parus major*) 6 and squirrel (*Sciurus vulgaris*) 8.

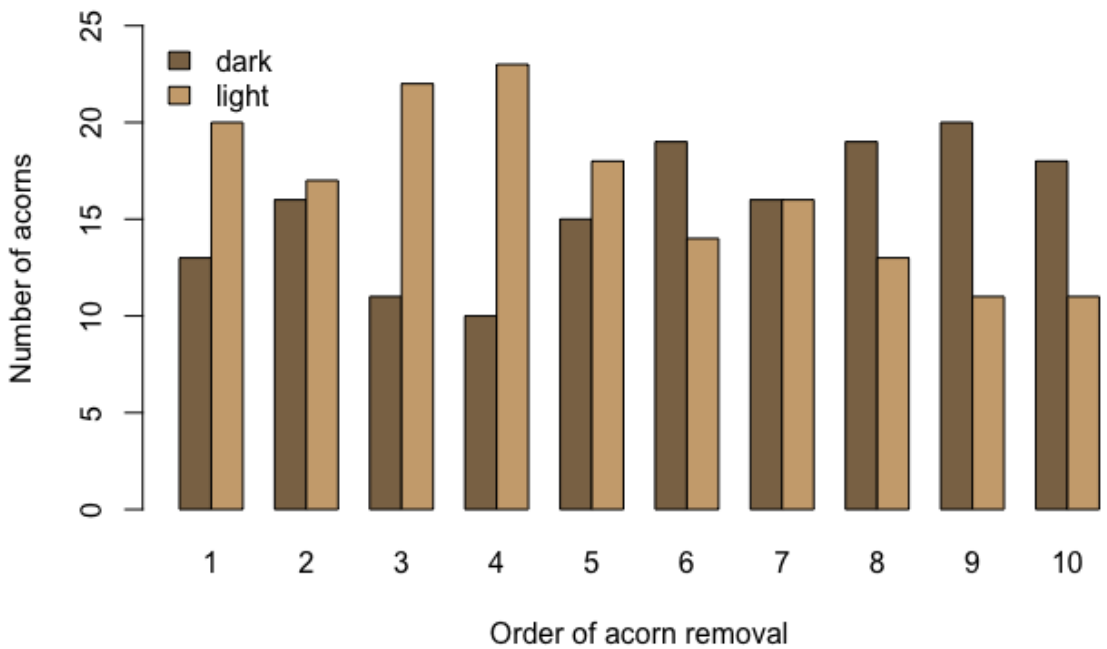


Figure 3 Number of dark brown and light brown acorns removed for each order in experiment one. I.e. order '1' means first choice, '2' second, and so on. In total 325 observations; Eurasian Jay (309), Eurasian nuthatch (2), Great tit (6), Squirrel (8).

Cafeteria experiment one – light vs. dark brown acorns

The present study was exclusively executed on the observations done by the Eurasian jays, as I wanted to establish if the jay preferred light brown acorns (H_1). The sample size is therefore 309 with a random factor of 5 localities for experiment one. Akaike's information criterion (AICc) was used to determine the best model (Burnham et al., 2011). The AICc for model 1 and 2 were very similar and could not determine the best model on its own. Model 1 had less parameters than model 2 and therefore gave the most parsimonious model (*table 2*).

Table 2 model selection based on AICc for experiment one (n = 309, random effect = 5 localities). (K = number of model parameters; AICc wt = AICc model weight; cum wt = cumulative model weight; LL = log-likelihood function). The model in bold is the most parsimonious model. For model specifications see Appendix 1.

	K	AICc	ΔAICc	AICc Wt	Cum Wt	LL
Model 2	5	400.31	0.00	0.61	0.61	-195.06
Model 1	**4**	**401.35**	**1.04**	**0.36**	**0.98**	**-196.61**
Model 3	3	406.97	6.66	0.02	1.00	-200.45
Model 4	3	434.2	34.01	0.00	1.00	-214.12

Model 1 included the number of light and dark brown acorns. The probability of choosing a light acorn was affected by the quantity of light and dark acorns present in the boxes (*table 3*).

Table 3 Parameter estimates from the multiple logistic regression model for model 1 in experiment one (n = 309, random effect = 5 localities) with the probability of choosing a light acorn as a function of number of light and dark acorns available.

Parameters	Estimate	SE	z	p
Intercept	-0.55	0.34	-1.62	0.11
No. of light acorns	0.53	0.10	5.23	**<0.001**
No. of dark acorns	-0.28	0.10	-2.78	**0.001**

The predictions from the model is given in figure 4. For each number of light acorn available, I predicted three probabilities based on how many dark acorns that were present. For the predictions I only chose maximum, median and minimum numbers of acorns present (five, three and one) to emphasize the results and to keep it simple. The probability of picking a light acorn was dependent on how many dark and light acorns that were present in the boxes. The probability of picking a light acorn over a dark acorn was higher for the following conditions (i.e. more than a fifty-fifty chance): 5 light acorns vs. all levels of dark acorns, 4 light acorns vs. 3 & 5 dark acorns, 3 light acorns vs. 5 dark acorns. At the start of the cafeteria experiment, with equal amount of light and dark acorns (i.e. 5 acorns in each box), the predicted probability of choosing a light acorn was 66%.

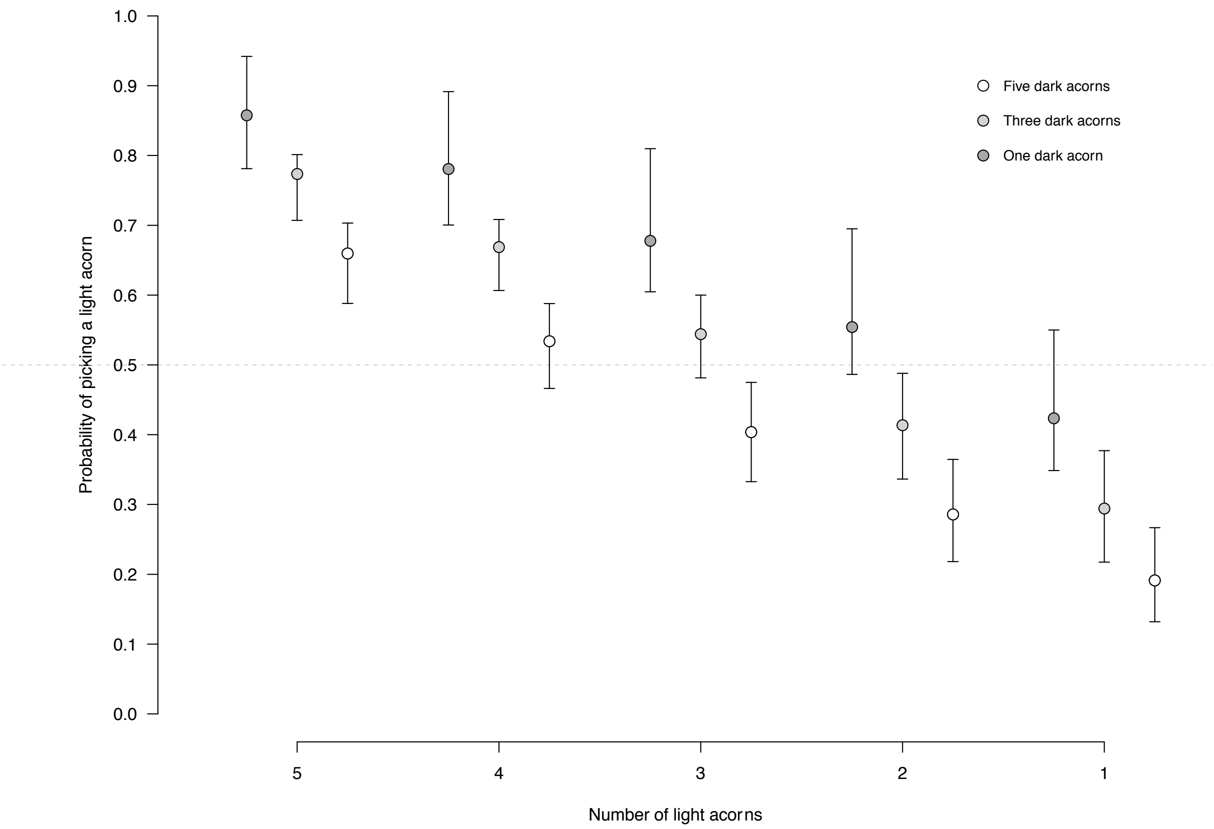


Figure 4 The probability that the Eurasian Jay (n = 309, random effect = 5 localities) are choosing a light acorn as a function of number of light acorns available in the box, for different combinations of number of dark acorns available (3 levels; one, three and five dark acorns), the logistic parameter estimates are given in table 2.

Acorn removal for experiment two – intact vs. non-intact acorns

Intact acorns were to a large extent chosen first. As the number of intact acorns decreased, more acorns with holes were chosen. Damaged acorns were mostly the last choice (*figure 5*). In total 356 were removed, from which Eurasian jay collected 321, squirrel 11, Eurasian nuthatch 11, great tit 2 and magpie (*Pica pica*) 8.

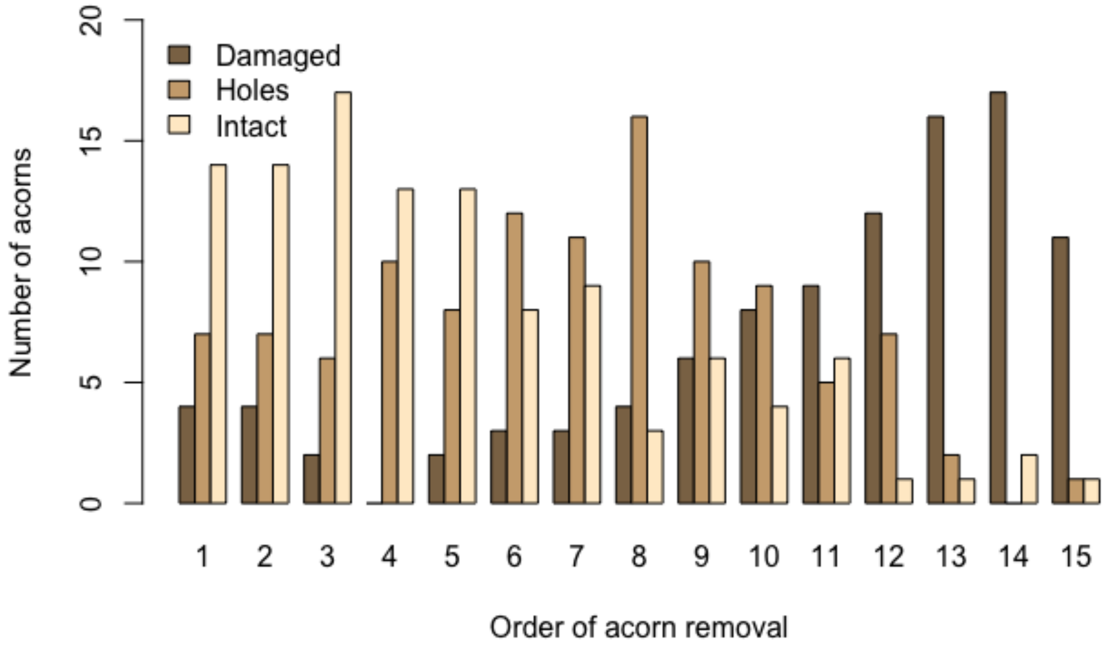


Figure 5 Number of acorns removed in each order for experiment two. I.e. order '1' means first choice, '2' means second choice and so on. In total 356 observations; Eurasian Jay (321), Squirrel (11), Eurasian nuthatch (11), Great tit (2), Magpie (8).

Cafeteria experiment two – intact vs. non-intact acorns

To test whether the Eurasian jay preferred intact acorns (H_2), observations of other species were excluded. The sample size was 321 but additional three acorns were removed, because there were only three of the same acorns available when the jay arrived, and therefore no choice could be done by the jay. The sample size is therefore 318, with a random effect of 5 localities. Model selection for experiment two was based on Akaike's information criterion (AICc). Model 2 was chosen to be the best model, because it had the lowest AICc (*table 4*) (Burnham et al., 2011).

Table 4 Model selection based on AICc for experiment two (n = 318). (K = number of model parameters; AICc wt = AICc model weight; cum wt = cumulative model weight; LL = log-likelihood function). The model in bold had the lowest AICc. For model specifications see Appendix 2.

	K	AICc	ΔAICc	AICc wt	Cum wt	LL
Model 2	**5**	**325.15**	**0.00**	**1**	**1**	**-157.48**
Model 4	3	336.74	11.59	0	1	-165.33
Model 7	5	340.60	15.45	0	1	-165.20
Model 1	5	340.61	15.46	0	1	-165.21
Model 3	5	340.61	15.46	0	1	-165.21
Model 5	3	382.05	56.90	0	1	-187.99
Model 8	5	385.83	60.68	0	1	-187.82
Model 6	3	414.07	88.92	0	1	-204.00

Model 2 included the number of intact acorns and the number of acorns with holes, and the interaction between them (*table 5*). The number of damaged acorns had no effect on the probability and were not included in the model (*table 4*).The number of intact acorns and acorns with holes present in the boxes, and the interaction between them had a significant effect on the probability of picking an intact acorn ($p<0.001$) (*table 5*).

Table 5 Parameter estimates from the multiple logistic regression model for experiment two (n = 318, random effect = 5 localities) with the probability of choosing an intact acorn as a function of the number of intact and non-intact acorns (acorns with holes and damaged acorns pooled), and the interaction between them.

Parameters	Estimate	SE	z	P
Intercept	-2.89	0.413	-6.992	**<0.001**
No. of intact acorns	1.45	0.246	5.890	**<0.001**
No. of acorns with holes	0.35	0.148	2.350	**0.01**
No. of intact acorns: No. of acorns with holes	-0.22	0.059	-3.721	**<0.001**

The predictions from the model is given in figure 6. For each intact acorn available, I predicted three probabilities based on how many non-intact acorns (acorns with holes and damaged pooled) that were present (maximum, median or minimum, five, three or one).

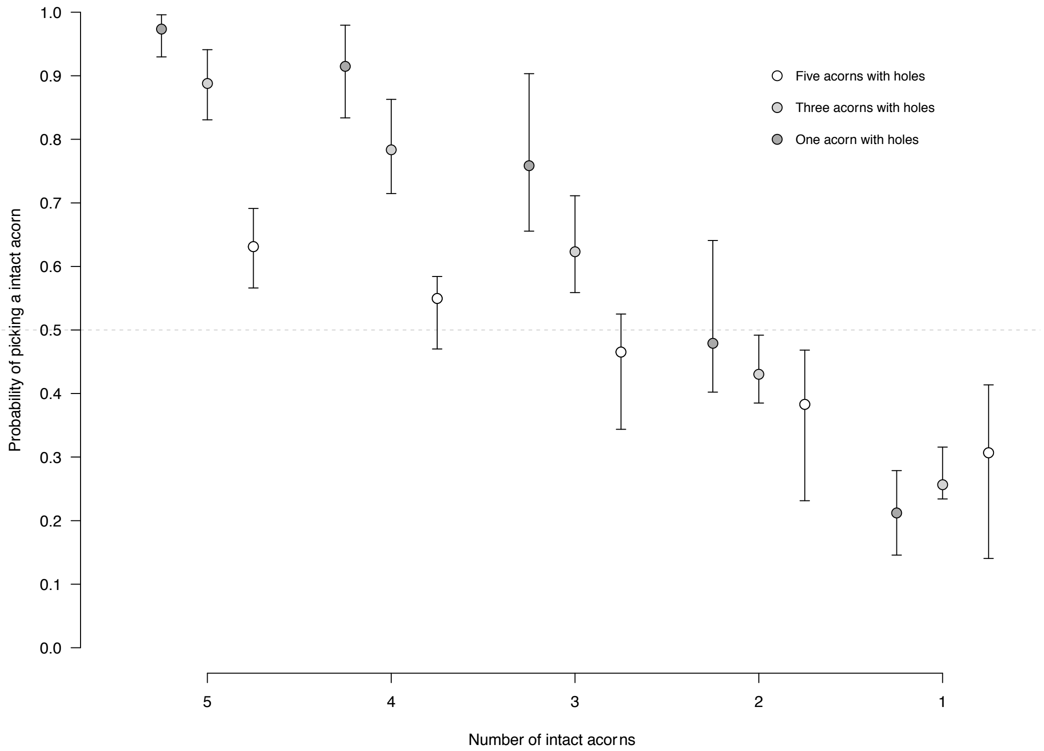


Figure 6 The probability that the Eurasian jay (n = 318) are picking an intact acorn as a function of the number of intact acorns available in the boxes, for different combinations of acorns with holes available (3 levels; one, three and five), logistic parameter estimates are given in table 4.

The probability of picking an intact acorn over a non-intact acorn was higher for the following conditions (i.e. more than a fifty-fifty chance): 5 intact acorns vs. all levels of acorns with holes, 4 intact acorns vs. all levels of acorns with holes, 3 intact acorns vs. 3 & 5 acorns with holes. Hence, the probability of picking an intact acorn decreased with lower number of intact acorns and higher number of acorns with holes available in the boxes, this could also be visualized by a three-dimensional plot (*figure 7*). At the start of the cafeteria experiment with equal numbers of intact acorns and acorns with holes (i.e. 5 acorns in each box) the predicted probability of picking an intact acorn was 63%. Note that this prediction was independent of the number of damaged acorns present in the box.

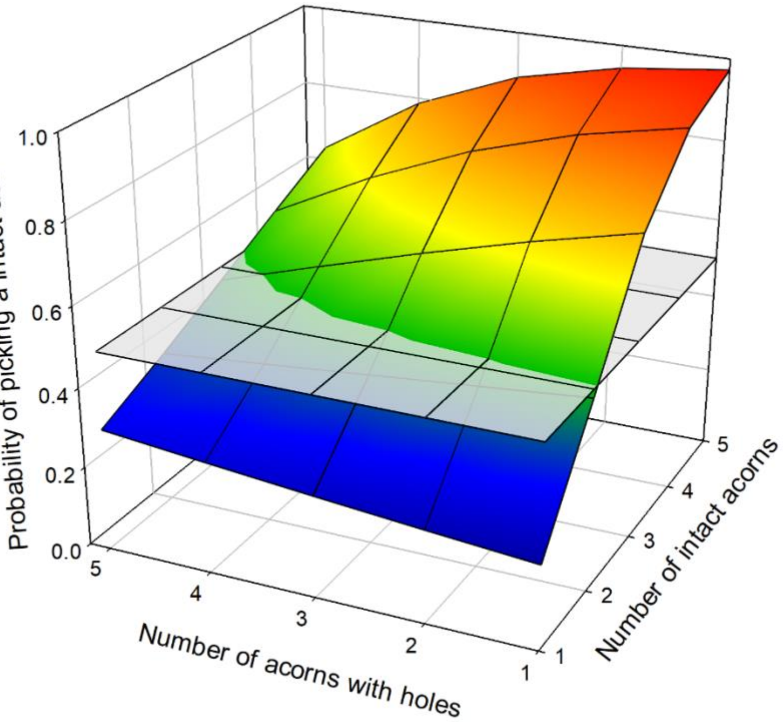


Figure 7 The probability that the Eurasian jay (N = 318) picking an intact acorn as a function of number of intact acorns and number of acorns with holes available, logistic parameter estimates are given in table 4. The grey horizontal plane represents fifty-fifty chance.

Discussion

The primary goal of this study was to identify if the Eurasian jay had any preference for acorns. I tested the hypotheses that the Eurasian jay preferred light acorns compared to dark brown acorns (H1) and that it preferred intact acorns over acorns with holes and damaged acorns (H2). The results showed that the Eurasian jay had a high preference for light brown (i.e. fresh) and intact acorns when there were many acorns available, but that it changed when those acorns were depleted. Therefore, both the quality and the quantity played a role in which acorns the jays chose.

First, I will discuss the results from the cafeteria experiment one. Next, I will discuss the results from the more complex cafeteria experiment two. I will then discuss which acorns the jays should cache. To conclude, I will discuss the limitations of the study and what can be done further on this topic.

Cafeteria experiment one

When all the acorns were available (i.e. 5 acorns in each box), there was a 66% probability that the Jay selected a light over a dark brown acorn, which supports the first hypothesis (H_1). There is no study available for direct comparison. However, Fleck & Woolfenden (1997) found that the wild scrub jays collected more green than brown acorns, both for caching and eating, in their study. 144 green acorns were cached and 64 were eaten. By comparison 75 brown acorns were cached and 16 were eaten (Fleck & Woolfenden, 1997). By contrast, Bossema (1979) found that more ripe, brown acorns were transported than green, unripe acorns. In his study, 23 brown acorns were transported, and 16 were not. Only 12 of his green acorns were transported, and 27 of the green acorns were not. As the green acorns also still hang on the trees, I think that the storage outcome for light brown acorns is a bit like the green acorns, and the retrieval of these would be similar. Further, the dark acorns in the experiment got a bit wrinkled, which can happen for overripe acorns.

Bossema suggested that the oaks benefit more from the collecting of ripe acorns, because he believed that the ripe acorns were more likely to produce strong seedlings (Bossema, 1979). However, in a study done on blue jays (*Cyanocitta cristata*), it was documented that collecting green acorns did not affect germination, as much as 88% of the green acorns that were collected germinated (Johnson & Adkisson, 1985).

Green and light acorns are often found in the trees, as they have not fully ripened yet and, therefore, have not fallen to the ground. If the jays begin collecting acorns early, they will be able to collect more acorns than if they were to start when the acorns are on the ground, often much later in the season (Jones, 1959). Beginning to collect acorns when they are still hanging on the trees can be an advantage, as there will be less competition from other animals that eat the acorns. There are many animals that feed on acorns as they contain fats, proteins and carbohydrates (Vander Wall, 2001). Therefore, the competition for this specific food can be very high, especially since it is only available for a limited time.

During the study, several other animals were documented eating the acorns in the cafeteria experiments. Squirrels, magpies, Eurasian nuthatches and great tits visited the locations and ate some of the nuts. In some of the cases, a whole dataset was removed due to squirrels removing all the nuts before the jay arrived. Taking acorns from the trees can therefore be advantageous for the jays, as there is less competition from ground dwelling animals such as rodents (*Rodere*) and deer (*Cervidae*) (Perea et al., 2011; Vander Wall, 1990). The dark brown acorns also have a higher chance of being moldy, as they have stayed on the ground longer (Schroder, 2002).

Florida scrub jays (*Aphelocoma coerulescens*) in DeGanges study also ate green acorns, but they only ate part of them. However, when the acorns were ripe the scrub jays consumed the whole acorn (DeGange et al., 1989). The green, unripe acorns contain high contents of tannins. Tannins are natural occurring acids and are a secondary metabolite in oaks. The basal part of the acorn containing the cotyledon contains lower proportions of tannins than the apical part, containing the embryo (Vander Wall, 2001). Acorn predators has been shown to selectively eat the basal parts of the acorns, leaving the higher containing apical part left (Steele et al., 1993). The scrub jay could selectively have eaten the basal part and left the apical part left. If so, the embryo could then be left to germinate later, as Johnson & Adkins (1985) showed that unripe acorns that were transported were able to germinate.

In the present study, the acorns that were used in cafeteria experiment one was stored inside a few weeks. The darker acorns got a bit wrinkled and lost their fresh-looking shell, which can happen to overripe acorns. What food type is stored and what is eaten is not random. Characteristics such as size, composition and perishability are common factors altering food caching behavior (Vander Wall, 1990). In an experiment on perishability on apples given to woodrats, they found that the dried apples were cached, and the fresher material was eaten

(Post & Reichman, 1991). The same result was found on a different study of woodrats, they preferred the perishable grapes over the acorns (Reichman, 1988). For long time storage, the animals should eat the high perishable food straight away and store less perishable food for later consumption (Gendron & Reichman, 1995). Another factor that can alter the food caching behavior is the germination rate. Squirrels in an experiment cached acorns and the difference in germination schedule strongly affected the caching preference (Smallwood et al., 2015).

To sum up cafeteria experiment one, the jays mostly preferred the light brown acorns, compared to the dark brown acorns. These results support the first hypotheses (H_1).

Cafeteria experiment two

Cafeteria experiment two was a more complex study than the first cafeteria experiment, as the jays had three choices. The choices were intact acorns, acorns with holes and damaged acorns.

For experiment two, there was a 63% probability that the Eurasian jay would select an intact acorn when all the acorns were present (i.e. 5 acorns in each box). Bossema registered the same result in his 1979 study. More sound acorns were transported by the jays compared to damaged acorns. Most of the acorns that are collected are being cached. A study done on radiotracking of acorns, showed that 64% of the acorns in the study was cached rather than eaten straight away by the jays (Pons & Pausas, 2007). Because most of the acorns are going into storage, they need to be in good condition, so they don't spoil before retrieval.

Because jays store acorns over a long period of time, it is important that the acorns are in good condition during retrieval. Sound acorns are less available for microbial attack (Vander Wall, 2010), and therefore, have a higher chance of being edible when the acorns are retrieved. To keep the acorns as viable as possible, the jays make a hole in the soil and push the acorn into it before covering the hole with litter. This technique is ideal for acorn survival (Crawley & Long, 1995), as this burial will leave the acorns away from ground pilferers and insects, and the moist soil will leave the acorns fresh for a longer period.

Unsound acorns can be parasitized by weevils, which is common attackers of the Quercus acorns (Steele et al., 1996; Vander Wall, 2001). Johnson & Adkins registered that unsound acorns were of no food value to their captive blue jays (Johnson & Adkisson, 1985). In the present study, the unsound acorns had drilled holes in them to mimic the holes that are naturally made by the weevil larvae. A study done on infested and sound acorns, showed that both infested and sound acorns were chosen, and that infested acorns were chosen even though sound acorns were present (Perea et al., 2012), like the present study. However, in a study done by Dixon, fewer acorns with holes were consumed by jays due to larvae infestation (Dixon et al., 1997). Some studies have tried to look whether the weevil larvae can be an additional food source for jays; however, Johnson & Adkins (1985) found that they were not. Even if the weevil is of no food value to the jays, the weevil-infested acorns do have a high percentage of germination (Branco et al., 2002).

Infested seeds have a reduced value because of extensive damage, lowered caloric value or reduced palatability (Steele et al., 1996). Weevil infestation can also act as a vector for fungal, bacterial, and viral infections (Vander Wall, 2001). Partial consumption by ground dwelling animals is also a common component that damages the acorns and may leave them more vulnerable to microbial attacks. *Ciboria batschiana* is the most common pathogen of oak acorns (Schroder, 2002). The higher tannin contents of the acorns, the more resistant the acorns were to the fungi (Takahashi et al., 2010). Unripe acorns contain higher levels of tannins than the ripe acorns. The riper the acorns, i.e. the longer the acorns have been on the ground, the higher the chance the fungi have to reach the acorn. Therefore, infested and moldy acorns would be less likely to survive storage then the non-infested acorns and acorns still hanging on the tree.

To sum up, the jays mostly preferred the sound acorns, but proceeded to eat the acorns with holes when there were fewer of the preferred sound acorns. The jays mostly avoided the partially damaged acorns or ate them when there were no other acorns left. These results support the second hypothesis (H_2).

What acorns should the jays choose?

A study done on several captive crows showed that they could wait for more preferred food items instead of eating the less preferred food (Hillemann et al., 2014). However, these birds were hand-raised from when they were young and are familiar with getting food every day. Wild birds encounter food irregularly, and the less preferred food items can be crucial for survival when the more preferred food items are scarce (Cueto et al., 2001), which is shown in the present study.

The jays encounter two decisions when food is available: 1) to consume the food or not, and 2) if they decide to consume it, whether to eat it straight away or cache it. A satiated animal should cache the food, and a hungry animal should consume the food immediately (Jacobs, 1992). An advantage of food storage is the opportunity to balance the food value of the food types as they change through time (i.e. ripe or spoil) (Gerber et al., 2004). To maximize the fitness, as optimal foraging theory suggests that the jays should cache acorns with a higher chance of giving an energetic reward. However, perishability is not the only factor when determining which acorn to choose. The handling time also matters. The items with the longest handling time should be cached (i.e. the sound acorns), and the acorns with less handling time should be eaten (Jacobs, 1992).

Creating artificial holes in the acorns could have decreased the handling time, which in turn could have influenced the decisions of the jays in the field (Davies et al., 2012). Acorns that have been on the ground for a long period of time might have a higher probability of being moldy or ripen faster than acorns that have just fallen from the trees or are taken straight from the trees. Sound acorns will also have a higher chance of being in a good condition over a longer period compared to partially damaged or damaged acorns, as they do not have the protection of the shell. And if the jays collect acorns on the ground, they should retrieve these acorns before they eat the acorns that were cached on the trees, as they will ripen faster.

Consumption of less preferred food items depends on the presence of preferred food items (Cueto et al., 2001). When the jay had removed the most preferred food items first, less of this item became available. Then they proceeded to take the less preferred food items (i.e. the damaged and with holes) as they were more abundant, as Cueto (2001) showed for captive Rufous-collared Sparrows (*Zonotrichia capensis*). The jay could eat the most preferred acorns first, and then take the rest of the acorns that was available for caching when the immediate nutritional demands were met. "Food hoarding animals continue harvesting seeds even when immediate nutritional demands are met" (Vander Wall, 1990). Typically, when an animal that stores food encounters a rich supply of nuts, it eats one or two and then stores the rest (Vander Wall, 2010). Bossema ended his study when half of the acorns were removed (Bossema, 1979). However, if he had continued the study, he might have encountered that most of the acorns were collected, like the present study.

Study limitations and future research

The first experiment is a very simple experiment. A simple test, such as experiment one shows a very simple way of looking at nature. There are very few times that a bird encounters just one type of acorn in the wild. Acorns have many different shapes and sizes, and this is a bit more controlled for in the second experiment. However, we have only looked at tree variables in the second experiment. Acorns can vary by nutrients, shapes, sizes and color. Some acorns can be infested, and others can be damaged. The second experiment, however, explains the choice a bit more, since it has three options to choose from and not only two. Experiment two is therefore a better study setup, since it is more realistic, but since it was a bit hard to analyze this, in theory it was only two choices: intact vs. non-intact acorns. To better understand the choices, a study done on multiple choices could be executed.

In both experiments the quantity of acorns had an effect in the model, and this was tested for in the model. The quantity was not a variable that I wanted to test for, but included, since it has been shown to have an effect. By including it in the model I could control the effect that it had. Since it had an effect, it would be interesting to look at this as a factor in future research.

Jays must both cache and eat acorns when they are foraging on acorns. This study did not look at which were consumed straight away, and which were cached. The jays might have eaten the more perishable food types, such as the acorns with holes, and have taken the intact acorns into storage, as the intact have a longer handling time. A study that distinguishes between caching and eating can further explain the choices made by jays, and their cognitive abilities.

Masting of oaks is also very common, and oaks have varying amounts of acorns each year. It would be interesting to see if there is a change in caching behavior when there are many acorns compared to less acorns. This would be a more complex study and would take more than one year to complete. However, there is a symbiosis between the jays and the oaks, but what is the benefit of not producing acorns each year, and what happens to the jays when the abundance of acorns is low?

Conclusion

In the present study quality of the acorn was important for the jays, although as the most preferred acorn were depleted the likelihood of collecting acorns of lower quality increased. There were two main hypotheses that I wanted to test for: H_1 – preference for light brown and fresh acorns compared to dark brown acorns, and H_2 – preference for intact acorns compared to damaged acorns and acorns with holes. In cafeteria experiment one, the jays had a higher preference for light brown acorns when there were many acorns available. In cafeteria experiment two, the jays had a preference for intact acorns. Both of the hypotheses were supported by these findings.

The results in this study stress the importance for good acorn years, which will yield more acorns, and by that, more food for the jays. Acorns that are partially damaged, have been parasitized by insects, or that have ripened early and fallen to the ground and are suspect to microbes, will less likely yield a successful retrieval, which means less food for the jays. By being selective when hoarding acorns, the jays could benefit from increased retrieval and possible positive fitness consequences.

Bibliography

Bossema, I. (1979). Jays and oaks: an eco-ethological study of a symbiosis. *Behaviour*, 70 (1-2): 1-116. doi: https://doi.org/10.1163/156853979X00016.

Branco, M., Branco, C., Merouani, H. & Almeida, M. H. (2002). Germination success, survival and seedling vigour of Quercus suber acorns in relation to insect damage. *Forest Ecology and Management*, 166 (1): 159-164. doi: https://doi.org/10.1016/S0378-1127(01)00669-7.

Brodin, A. (2010). The history of scatter hoarding studies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365 (1542): 869-881. doi: 10.1098/rstb.2009.0217.

Burnham, K. P., Anderson, D. R. & Huyvaert, K. P. (2011). Erratum to: AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology*, 65 (2): 415-415. doi: 10.1007/s00265-010-1084-z.

Chettleburgh, M. (1952). Observations on the collection and burial of acorns by jays in Hainault Forest. *British birds*, 45 (35): 359-364.

Clayton, N. S. & Dickinson, A. (1998). Episodic-like memory during cache recovery by scrub jays. *Nature*, 395 (6699): 272-274. doi: 10.1038/26216.

Crawley, M. J. & Long, C. R. (1995). Alternate bearing, predator satiation and seedling recruitment in Quercus robur L. *Journal of Ecology*, 83 (4): 683-696. doi: 10.2307/2261636.

Cueto, V., Marone, L. & Casenave, J. (2001). Seed preferences by birds: Effects of the design of feeding-preference experiments. *Journal of Avian Biology*, 32: 275-278. doi: 10.1111/j.0908-8857.2001.320311.x.

Davies, N. B., Krebs, J. R. & West, S. A. (2012). An introduction to behavioural ecology.

DeGange, A. R., Fitzpatrick, J. W., Layne, J. N. & Woolfenden, G. E. (1989). Acorn harvesting by Florida scrub jays. *Ecology*, 70 (2): 348-356. doi: 10.2307/1937539.

Dixon, M. D., Johnson, W. C. & Adkisson, C. S. (1997). Effects of weevil larvae on acorn use by blue jays. *Oecologia*, 111 (2): 201-208. doi: 10.1007/s004420050226.

Emery, N. J. & Clayton, N. S. (2004). The mentality of crows: convergent evolution of intelligence in Corvids and Apes. *Science*, 306 (5703): 1903-1907. doi: 10.1126/science.1098410.

Fleck, D. C. & Woolfenden, G. E. (1997). Can acorn tannin predict Scrub-jay caching behavior? *Journal of Chemical Ecology*, 23 (3): 793-806. doi: 10.1023/b:joec.0000006411.68081.14.

Free, J. B. & Williams, I. H. (1972). Hoarding by honeybees (Apis mellifera L.). *Animal Behaviour*, 20 (2): 327-334. doi: 10.1016/s0003-3472(72)80054-x.

Gendron, R. P. & Reichman, O. J. (1995). Food perishability and inventory management: a comparison of three caching strategies. *The American Naturalist*, 145 (6): 948-968. doi: 10.1086/285778.

Gerber, L. R., Reichman, O. J. & Roughgarden, J. (2004). Food hoarding: future value in optimal foraging decisions. *Ecological Modelling*, 175 (1): 77-85. doi: https://doi.org/10.1016/j.ecolmodel.2003.10.022.

Gómez, J. M. (2003). Spatial patterns in long-distance dispersal ofQuercus ilexacorns by jays in a heterogeneous landscape. *Ecography*, 26 (5): 573-584. doi: 10.1034/j.1600-0587.2003.03586.x.

Grodzinski, U. & Clayton, N. S. (2010). Problems faced by food-caching corvids and the evolution of cognitive solutions. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365 (1542): 977-987.

Haftorn, S. (1971). *Norges fugler*. Oslo: Universitetsforlaget.

Hillemann, F., Bugnyar, T., Kotrschal, K. & Wascher, C. A. F. (2014). Waiting for better, not for more: corvids respond to quality in two delay maintenance tasks. *Animal behaviour*, 90: 1-10. doi: 10.1016/j.anbehav.2014.01.007.

Jacobs, L. F. (1992). The effect of handling time on the decision to cache by grey squirrels. *Animal Behaviour*, 43 (3): 522-524. doi: https://doi.org/10.1016/S0003-3472(05)80111-3.

Janick, J. & Paull, R. E. (2008). *The encyclopedia of fruit and nuts*: CABI.

Johnson, W. C. & Adkisson, C. S. (1985). Dispersal of Beech nuts by Blue jays in fragmented landscapes. *The American Midland Naturalist*, 113 (2): 319-324. doi: 10.2307/2425577.

Jones, E. W. (1959). Quercus L. *Journal of Ecology*, 47 (1): 169-222. doi: 10.2307/2257253.

Madge, S. & Burn, H. (1994). *Crows and jays: a guide to the crows, jays and magpies of the world*: Christopher Helm.

McNamara, J. M. & Houston, A. I. (1985). Optimal foraging and learning. *Journal of Theoretical Biology*, 117 (2): 231-249. doi: https://doi.org/10.1016/S0022-5193(85)80219-8.

Perea, R., Miguel, A. S. & Gil, L. (2011). Flying vs. climbing: Factors controlling arboreal seed removal in oak–beech forests. *Forest Ecology and Management*, 262 (7): 1251-1257. doi: https://doi.org/10.1016/j.foreco.2011.06.022.

Perea, R., San Miguel, A., Martínez-Jauregui, M., Valbuena-Carabaña, M. & Gil, L. (2012). Effects of seed quality and seed location on the removal of acorns and beechnuts. *European Journal of Forest Research*, 131 (3): 623-631. doi: 10.1007/s10342-011-0536-y.

Pons, J. & Pausas, J. G. (2007). Acorn dispersal estimated by radio-tracking. *Oecologia*, 153 (4): 903-911. doi: 10.1007/s00442-007-0788-x.

Post, D. & Reichman, O. J. (1991). Effects of food perishability, distance, and competitors on caching behavior by Eastern woodrats. *Journal of Mammalogy*, 72 (3): 513-517. doi: 10.2307/1382134.

Reichman, O. J. (1988). Caching behaviour by eastern woodrats, Neotoma floridana, in relation to food perishability. *Animal Behaviour*, 36 (5): 1525-1532. doi: https://doi.org/10.1016/S0003-3472(88)80223-9.

Roberts, R. C. (1979). The evolution of avian food-storing behavior. *The American Naturalist*, 114 (3): 418-438.

Schroder, T. (2002). On the geographic variation of Ciboria batschiana (Zopf) Buchwald, the main pathogenic fungus on acorns of Quercus robur and Q. petraea in Europe. *Dendrobiology*, 47.

Selås, V. (2017). Autumn irruptions of Eurasian Jay (*Garrulus glandarius*) in Norway in relation to acorn production and weather. *Ornis Fennica*, 94: 92–100.

Smallwood, P. D., Steele, M. A. & Faeth, S. H. (2015). The ultimate basis of the caching preferences of rodents, and the oak-dispersal syndrome: tannins, insects, and seed germination. *American Zoologist*, 41 (4): 840-851. doi: 10.1093/icb/41.4.840.

Smith, C. C. & Reichman, O. J. (1984). The evolution of food caching by birds and mammals. *Annual Review of Ecology and Systematics*, 15 (1): 329-351. doi: 10.1146/annurev.es.15.110184.001553.
Stapanian, M. A. & Smith, C. C. (1978). A model for seed scatterhoarding: coevolution of Fox squirrels and black walnuts. *Ecology*, 59 (5): 884-896. doi: 10.2307/1938541.
Steele, M. A., Knowles, T., Bridle, K. & Simms, E. L. (1993). Tannins and partial consumption of acorns: implications for dispersal of oaks by seed predators. *The American Midland Naturalist*, 130 (2): 229-238. doi: 10.2307/2426123.
Steele, M. A., Hadj-Chikh, L. Z. & Hazeltine, J. (1996). Caching and feeding decisions by sciurus carolinensis: responses to weevil-Infested acorns. *Journal of Mammalogy*, 77 (2): 305-314. doi: 10.2307/1382802.
Steen, R., Austad, A.-M., Johnny, S. & Bjerke, B. A. (2017). Daily activity and nest attendance in a breeding pair of Parrot Crossbills <i>Loxia pytyopsittacus</i> in southern Norway. *Ornis Norvegica*, 40: 24. doi: 10.15845/on.v40i0.1206.
Stephens, D. W. & Krebs, J. R. (1986). *Foraging theory*, vol. 1: Princeton University Press.
Takahashi, A., Ichihara, Y., Isagi, Y. & Shimada, T. (2010). Effects of acorn tannin content on infection by the fungus Ciboria batschiana. *Forest Pathology*, 40 (2): 96-99. doi: 10.1111/j.1439-0329.2009.00612.x.
Vander Wall, S. B. (1990). *Food Hoarding in Animals*: University of Chicago Press.
Vander Wall, S. B. (2001). The evolutionary ecology of nut dispersal. *The Botanical Review*, 67 (1): 74-117. doi: 10.1007/bf02857850.
Vander Wall, S. B. (2010). How plants manipulate the scatter-hoarding behaviour of seed-dispersing animals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365 (1542): 989-997. doi: 10.1098/rstb.2009.0205.
Wilson, D. & Janzen, D. (1972). Predation on Scheelea palm seeds by Bruchid beetles: seed density and distance from the parent palm. *Ecology*, 53: 954. doi: 10.2307/1934315.

Appendix

Appendix 1 Model predictions for cafeteria experiment one.

```
Trial1$Choice_light<-as.factor(Trial1$Choice_light)

m1 <- glmer(Choice_light ~ Light_count+Dark_count + (1 | Place), data = Trial1,
            family = binomial(link = "logit"))

m2 <- glmer(Choice_light ~ Light_count*Dark_count + (1 | Place), data = Trial1,
            family = binomial(link = "logit"))
m3 <- glmer(Choice_light ~ Light_count + (1 | Place), data = Trial1,
            family = binomial(link = "logit"))
m4 <- glmer(Choice_light ~ Dark_count + (1 | Place), data = Trial1,
            family = binomial(link = "logit"))
```

Appendix 2 Model predictions for cafeteria experiment two.

```
Trial2$Choice_intact<-as.factor(Trial2$Choice_intact)

m1 <- glmer(Choice_intact ~ Intact_count+Hole_count+Damaged_count + (1 | Place), data = Trial2,
            family = binomial(link = "logit"))

m2 <- glmer(Choice_intact ~ Intact_count*Hole_count + (1 | Place), data = Trial2,
            family = binomial(link = "logit"))
m3 <- glmer(Choice_intact ~ Intact_count+Hole_count+Damaged_count + (1 | Place), data = Trial2,
            family = binomial(link = "logit"))
m4 <- glmer(Choice_intact ~ Intact_count + (1 | Place), data = Trial2,
            family = binomial(link = "logit"))
m5 <- glmer(Choice_intact ~ Hole_count + (1 | Place), data = Trial2,
            family = binomial(link = "logit"))
m6 <- glmer(Choice_intact ~ Damaged_count + (1 | Place), data = Trial2,
            family = binomial(link = "logit"))
m7 <- glmer(Choice_intact ~ Intact_count*Damaged_count + (1 | Place), data = Trial2,
            family = binomial(link = "logit"))
m8 <- glmer(Choice_intact ~ Hole_count*Damaged_count + (1 | Place), data = Trial2,
            family = binomial(link = "logit"))
```

Norges miljø- og biovitenskapelige universitet
Noregs miljø- og biovitskapelege universitet
Norwegian University of Life Sciences

Postboks 5003
NO-1432 Ås
Norway