Norwegian University of Life Sciences
Faculty of Environmental Science and Technology
Department of Ecology and Natural Resource Management

Master Thesis 2014
30 credits

# Assessing prey delivery and handling in Tengmalm´s owl (Aegolius funereus) by video surveillance at nest

# Bestemmelse av byttedyr levering og håndtering hos perleugle (Aegolius funereus) ved videoovervåking i reir

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# Preface

This Master thesis is part of my master degree in natural resource management. Working with this thesis have been a valuable experience and educational process, which gave me good insight in raptorial behavior as well as scientific work. I would like to thank my main supervisor professor Geir A. Sonerud for excellent guidance through this entire period. You have been a great support and spent numerous hours helping me in the field as well as in the writing process with identification of prey items delivered at the nest, statistical support, and by reviewing my drafts. I will also thank my additional supervisor Ronny Steen for technical and statistical support, help with illustrations and comments on my final draft. Another one deserving thanks is my fellow student Rune Sørås for great cooperation during field work and for all support during the master period.

I would like to thank the Norwegian Environment Agency which financially supported my field work, and Vidar Selås for help with identifying avian prey. Last but not least, I want to thank my parents for letting me barrow the car during field work, and my partner Sigmund Rolfsjord for all help and support during the whole master period.

Norwegian University of Life Sciences, May 2014

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## Abstract

Prey delivery and handling at four Tengmalm's owl (*Aegolius funereus*) nests was assessed by video monitoring in an increase year for the vole population. A total of 179 prey items was recorded delivered at the nest, and 121 of those where identified as voles. *Microtus* voles (Field vole (*Microtus agrestis*) and Root vole (*Microtus oeconomus*) pooled) made up 39% of the prey items and 51% of the prey mass, suggesting that these were the most important prey. Bank vole (*Myodes glareolus*) was delivered relatively more often early in the season, and in the morning hours, whereas *Microtus* voles were a more frequent prey among the delivered prey items late in the season. The Tengmalm's owl tended to deliver prey items in runs, as prominent in a win-stay strategy, and shrews (*Sorex sp.*) were the most likely prey hunted by use of this strategy. Whether a prey was decapitated prior to delivery at the nest was affected by prey body mass and time since solar midnight (SM), where the probability of decapitation increased with prey body mass and time since SM. Prey handling at the nest was conducted by the female until the nestlings were 18 days old. They were then able to handle the prey items independently.

# Sammendrag

Levering og håndtering av byttedyr hos fire hekkende perleugler (*Aegolius funereus*) ble undersøkt ved videoovervåking i et år med økende smågnagerbestand. Totalt ble 179 byttedyr registrert levert på reiret, og 121 av disse var smågnagere. *Microtus* gruppen (Markmus (*Microtus agrestis*) og fjellrotte (*Microtus oeconomus*) slått sammen) var mest tallrik med 39% av byttedyrene og 51% av byttedyrmassen, noe som tyder på at *Microtus* var det viktigste byttedyret. Klatremus (*Myodes glareolus*) ble oftere levert tidlig i sesongen, og på morgenen snarere enn på kvelden, mens *Microtus* var vanligere blant de leverte byttedyrene sent i sesongen. Perleugla hadde en tendens til å levere like byttedyr typer etter hverandre, et trekk som er fremtredende i en "win-stay" strategi, og spissmus var det byttedyret som mest trolig ble jaktet ved bruk av denne strategien. Sannsynligheten for dekapitering av et byttedyr før levering på reiret var påviket av byttedyrets vekt og tid siden solar midnatt (SM), der sannsynligheten for dekapitering økte med byttedyret vekt og tid siden SM. Byttedyrhåndtering på reiret ble utført av hunnen frem til ungene var omkring 18 dager gamle. De var da store nok til å håndtere byttedyret på egenhånd.

## Contents

# 1.0 Introduction

The diet of predators has been well studied through decades as a way to understand population fluctuations, and behavioral patterns of both predator and prey (Eldegard & Sonerud 2010; Korpimäki 1985; Sonerud et al. 2014). Knowledge is essential in order to understand the predator's role in the ecosystem and conduct sustainable management of the predators and their prey. In raptorial birds (hawks, falcons and owls) foraging success and nest predation are the two major factors affecting the birds fitness (Hakkarainen et al. 1997; Sonerud 1985a). According to optimal foraging theory, a raptor should maximize its net rate energy intake, and therefore select some species and avoid others (Stephens & Krebs 1986). The profitability of a prey item is measured as its energetic value per time spent capturing, preparing and ingesting the prey i.e. per handling time, suggesting that prey items with the highest energy content and lowest handling time is the most profitable prey (Stephens & Krebs 1986), as handling time in raptors often is extended and energy demanding (Slagsvold & Sonerud 2007).

Many birds bring back their prey to fixed locations, termed central place foraging (Sodhi 1992). Central place foraging is widespread among raptors during breeding season, making it possible to record the prey deliveries by use of video technology. Many birds are multiple prey loaders (Orians & Pearson 1979), meaning they return to the nest with several prey at a time, often taken from different habitats. This makes it hard to identify species, and also determine the order in which they were caught or what habitat they were taken from. Raptorial birds however, are single-prey loaders (Orians & Pearson 1979), carrying only one prey item at the time from capture site to the nest (Sonerud 1985b), making it easy to identify the item to species, and determine approximately when it was caught. Larger prey items are transported more often than the smaller ones, which are consumed at the capture site, as the items with energy values below a certain level are not worth transporting (Andersson 1981; Sonerud 1992).

Tengmalm's owl (*Aegolius funereus*) is a single prey loader, and therefore a suitable study species for video monitoring during nesting when it is a central place forager. It is also a common owl and is not disturbed too easily. Tengmalm's owl often use artificial nest boxes as nesting sites, which make it easy to assemble a small camera inside a nest box and record the prey deliveries and handling behavior.

The Tengmalm's owl, known as the boreal owl in America, is a small owl which weighs c.100 g. It is nocturnal (Korpimäki & Hakkarainen 2012) and occurs in boreal and subalpine forests in an almost continuous circumboreal distribution that extends from Scandinavia eastward across the northern forests of Siberia and from Alaska across Canada to the Atlantic (Hayward 1994; Koopman et al. 2005), and is probably the most frequent bird of prey in Fennoscandian coniferous forests (Korpimäki & Norrdahl 1989). The Tengmalm's owl primarily feeds on voles (Hakkarainen et al. 1997; Korpimäki 1988; Zárybnická et al. 2013). In northern Fennoscandia the vole population follows a cycle with peaks usually every 3-4 years (Hakkarainen et al. 1997), and breeding performance and nestling survival is largely dependent on the fluctuations of microtine (Hakkarainen et al. 1997). In good vole years the egg-laying starts earlier and clutches are larger than in years of low vole abundance, when small birds (< 120 g) and shrews (Soricidae) counts as a larger part of the owls diet (Hakkarainen et al. 1997; Korpimäki 1988; Korpimäki & Norrdahl 1989). The Tengmalm's owl uses a low-perched sit-and-wait hunting technique, an adaptation for foraging in woodlands (Bye et al. 1992), and seems to prefer open ground and edges of woodlands for hunting sites (Korpimäki 1988). This is also the preferable habitat for *Microtus* voles, and may indicate that these are a more profitable prey for Tengmalm's owl than those in the woodlands (Korpimäki 1988). The male is the sole provider in this species, until late nestling period (Eldegard & Sonerud 2009, 2010, 2012; Santangeli et al. 2012).

The Tengmalm's owl might be the most studied owl in Fennoscandia and much is known about the biology and ecology of this species (Korpimäki & Hakkarainen 2012). However, prey handling before and after delivery at nest has been given less attention, even though it is considered a relevant part of the predator's total foraging activities.

I wanted to study the Tengmalm's owl's prey handling behavior from prey delivery at the nest to nestling prey ingestion, and to understand which factors that contributed to the delivery of specific prey items. In order to do so, I video monitored the Tengmalm's owls prey deliveries at the nest during a breeding season.

My aims for this thesis were to: 1) Analyze the importance of different prey groups in the Tengmalm's owl's diet during breeding season. 2) Find out if any hunting strategy seemed prominent in the owl or if any prey items tended to be delivered in "runs". 3) See what kind of handling the prey were given prior to delivery at the nest, and test which factors influenced decapitation of prey prior to delivery. 4) Analyze prey handling and parental behavior in the nest and see how the feeding behavior of the nestlings changed throughout the season.

# 2.0 Materials and methods

## 2.1 Study area

The field work was conducted from May - July 2013 in Hedmark county, SE Norway. Of the four nest studied three were in Vang Almenning in Hamar municipality (60° 56′ N, 11°08′ E), and one was in Elverum municipality (60° 52′ N, 11° 33′ E). The study area is part of the northern boreal forest with spruce (*Picea abies*), pine (*Pinus sylvestris*) and birch (*Betula pubescens*) dominating the tree cover. Field layer includes shrubs of willow (*salix sp*.), bilberry bushes (*Vaccinium myrtillus*) and small ferns (Pteridophyta), while mosses (Bryophyta) cover the forest floor. The humidity is high, resulting in numerous bugs. Annual precipitation is 700-800 mm (Selås et al. 2013) and the precipitation in May-July 2013 was 147 mm, 120.5 mm and 40.8 mm with a normal of 44 mm, 77 mm and 73 mm in May-June. The forest is characterized by cultivation in forms of clear-cuts, forest roads and spruce plantations in addition to some outfield grazing by different livestock. The altitude varied from 400 m above sea level at the nest site in Elverum, to 500 – 600 m above sea level in Vang Almenning. The forest floor is normally snow covered from November to May (Selås et al. 2013).

The four nests studied were in nest boxes made of wooden boards. Each nest box was mounted in a pine tree 5 m above ground, and the box at location 2 and 3 had a metal plate around the trunk of the tree below the box to prevent predation from the pine marten (*Martes martes*) which is an important predator on Tengmalm's owls nests (Sonerud 1985a). Brood sizes at the start of filming was 3, 5, 4, 4 nestlings.

## 2.2 Available prey

Year 2013 was expected to be an increase year for the vole population, and 2014 to be a peak year (G. A. *Sonerud pers. comm.*). In order to determine vole abundance and local inequalities, trapping indexes from Hamar and Elverum municipalities were obtained. The trapping was done in Hamar municipality from 11-15 May, and in Elverum from 23-27 June by permission from the Norwegian environment agency (G. A. Sonerud pers. comm.). Both locations had fluctuating populations of *Microtus* voles, bank vole (*Myodes glareolus*), wood lemming (*Myopus schisticolor*) and shrew. Nest site 1 had also a population of birch mouse (*Sicista betulina*) (Heggland & Sonerud 1998). The trapping indexes showed highest abundance of bank voles and *Microtus* voles in Hamar, with low indexes for shrews and wood lemming. In Elverum bank vole and wood lemming had the highest abundances, followed by *Microtus* voles and shrews. The trappings in Elverum were done some distance away from the nesting site, and were therefore considered indicative (G. A. Sonerud pers. comm.). The Tengmalm's owl's hunting territories was also breeding site for many birds, including passerines (Passeriformes) like sylvids (Sylviidae) and thrushes (Turdidae).

## 2.3 Video monitoring and analyses

To video monitor the nests with as little interference as possible a camera system was integrated into a roof for the nest box, containing a waterproof plastic container for the camera and an infrared light (IR-light). When assembling the camera equipment in the evening, the camera was easily inserted into the roof, and the roof was exchanged with the one at the chosen nest box. A GoPro camera (Hero 3, white edition) was used as recording equipment. The camera could film continuously for about 7-12 hours depending on resolution, and was charged after every night of filming. An SD-card with 32 GB was used as memory card, and was removed every morning to transfer the data to a computer and control the quality of the recorded movie. To supply power, the IR-light was connected by a 30 cm cord to a sealed 12 VDC battery (small MC-battery) that was put on top of the nest box roof.

The camera was switched on about 22:00 p.m, and switched off about 03:30 a.m. Simultaneously with the filming, the male at each nest monitored was radio-tracked on foot during the night (Sørås 2014). On the nights when the IR-light failed or the resolution on the videotape was poor, I was able to control the assumed deliveries with observations from the radio tracking to make sure the deliveries were correct.

On nights with heavy rain no filming was performed out of concern for damaging the camera equipment. In total, the nests were filmed on 29 nights, but one night was excluded because the nestling had fledged and the nest box was empty. Two nights of filming resulted in completely dark picture frames due to failure of the IR-light, but deliveries was nevertheless detected by listening to the audio track and determine deliveries when the female and nestlings where making a lot of noise. These prey items was put in the category of unidentified prey and were excluded from the statistical tests, but one was identified by help from the field data. In total there were 162 hours and 22 minutes of usable film, distributed unequally on the four nests. Weather conditions and age of the nestlings influenced which nest to film, and consequently some nests were filmed more often than others. When estimating prey delivery rates at the different nests, the total prey mass delivered at each nest was divided by the total hours filmed at the nest, to correct for uneven recording time.

Information about temperature and precipitation was obtained from Rena airport weather station (eKlima 2014), and was used for all the different nest sites. However, because nights with heavy rain usually was left out, the nights with precipitation recorded were too few to be used in the statistical analyses.

## 2.4 Establishing prey species and body mass

After all the video clips with prey deliveries had been sorted out from the main video, the clips were run  in slow motion and all prey items recorded delivered at the nest were identified to the lowest taxonomical level possible. Specific traits like tail length and fur color were used to identify the different prey species. Some prey items was impossible to identify due to loss of species specific traits after being handled by the male, or because it was hidden underneath a parent owl during delivery, or by begging nestlings. Field voles (*Microtus agrestis*) and root voles (*Microtus oeconomus*) were pooled as *Microtus* voles because of difficulties in distinguishing one from the other on a video clip. Different species of shrews were pooled as shrews (*Sorex sp*.) for the same reason.

All prey items of the same species were assigned the same body mass, taken as an average body mass based on trapped animals (G. A. Sonerud pers. obs.). For prey items identified to higher taxa, a mean body mass was calculated by adding all the under categories and dividing them on the total amount of prey items in that group. This was done for items in the categories vole (Microtinae), rodent and small mammal.

All decapitated prey items were listed, and the time of prey delivery was noted. I also recorded whether a prey item delivered at the nest was the same species as the previous item, to see if the owl returned to the location where it last hunted successfully, indicating a win-stay hunting strategy (Sonerud 1985b).

## 2.5 Feeding behavior

Of the delivered prey items at the nest sites, 148 were registered as plucked or swallowed by the female or the nestlings during the breeding period. The item was registered as handled by the female if she was the only one plucking it and feeding morsels to the nestlings. If the nestlings where the only ones plucking the item or swallowing it, it was registered as handled by the nestlings. If both the nestlings and the female plucked the prey or the female plucked it and one nestling swallowed it later, it was considered handled by the female. Only 12 instances where both handled the prey item were registered. I also attempted to estimate handling time for each prey item, but because the nest box contained more than one prey item at a time, it was impossible to tell which prey was handled, as it was hidden underneath the female or nestlings during the handling time.

## 2.6 Statistics

My statistical analyses was performed with the software JMP, version 10 (SAS 2012) and the software R version 3.0.3 (R Development Core Team 2014). Linear regression analysis was done in JMP and used for my raw data. Logistic multilevel regression was done in R, where I used generalized linear mixed-effects models (glmer), by the Laplace approximation in the lme4 package (Zuur et al. 2009). Binominal distribution was used on all tests run in R (Gilmour et al. 1985), and nest ID was random factor in all my analyses to control for interpair variation, except one nominal logistic test performed in JMP, where the observations of specific prey types were too unevenly distributed at the four nests to allow using nest ID as random factor. This applied for the win-stay analyses, where the deliveries of shrews especially, were overrepresented at one nest site and absent in another, resulting in improper measurements when correcting for nest ID. I therefore did a likelihood-ratio analyses and a Pearson analyses in JMP to estimate the probability of delivering prey items in runs at each nest. The results were then combined in a meta-analyses by use of Fischer´s combined probability test to test the general tendency towards delivering prey items in runs.

Overall 8 different tests where run, using different response variables and explanatory variables as shown in Table 1. Non-significant explanatory variables were removed in a backward selection procedure, and the remaining significant variables are presented. Tests with no significant values are excluded from the results.

**Table 1:** Explanatory variables for which each response variable was tested. Eight tests were run. An X means that the variable was tested for, and a dash means that the variable was not tested for. Each prey category (*Microtus* voles, wood lemming, bank vole and shrew) denotes whether the prey type or any other prey type was delivered. Decapitation denotes whether a prey item was decapitated prior to delivery. Same type as previous item is a yes or no response to whether or not the delivered prey was the same type as the last that was delivered at the nest. Type of current prey item denotes the prey category of the current delivered prey item. Prey handler denotes whether the prey item was handled by the female or the nestlings after delivery. Nest ID is used as random factor in all tests (n=4).

| Explanatory variables | Response variables | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | *Microtus* voles | Wood lemming | Bank vole | Shrew | Decapitation | Same type as previous item | Type of current prey item | Prey handler |
| Temperature | X | X | X | X | X | _ | _ | _ |
| Date | X | X | X | X | X | _ | _ | _ |
| Minutes from SM | X | X | X | X | X | _ | _ | _ |
| Before or after SM | X | X | X | X | X | _ | _ | _ |
| Delivery time | X | X | X | X | X | _ | _ | _ |
| (Delivery time)$^2$ | X | X | X | X | X | _ | _ | _ |
| Nestling age at delivery | X | X | X | X | X | _ | _ | X |
| Prey body mass | _ | _ | _ | _ | X | _ | _ | X |
| Prey category | _ | _ | _ | _ | _ | X | _ | _ |
| Type of previous prey item | _ | _ | _ | _ | _ | _ | X | _ |
| Time since previous delivery | _ | _ | _ | _ | _ | X | _ | _ |

Temperature = ambient temperature ($^o$C) at the time of the prey delivery. Date = the day of the prey delivery taken as number of days after 31 May. Minutes from SM = number of minutes elapsed between solar midnight and prey delivery. Before or after SM = whether prey was delivered before (evening) or after (morning) solar midnight. Delivery time = time of prey delivery, measured linearly from 0800 PM. (Delivery time)$^2$ = time of prey delivery, squared to control for non-linear effects. Nestling age at delivery = age of the oldest nestling at the time of prey delivery. Prey body mass = estimated body mass of the delivered prey item. Prey category= Prey category of previous delivered prey (bank vole, *Microtus* vole, wood lemming or shrew). Type of previous prey item = whether a delivered prey was the same type as the previous delivered prey. Time since previous delivery = Number of seconds elapsed from previous delivery.

# 3.0 Results

## 3.1 Prey delivery at the nest

A total of 179 prey items were recorded delivered at the four nests. Of these, 39 were identified to species, 117 to genus, 20 to a higher taxonomical level, whereas three prey items were unidentified (Table 2). All identified prey were either vole or shrew, except four birds.

**Table 2:** Prey delivered by male Tengmalm's owl, at each nest box ID (1-4)

| | Nest ID | | | | |
|---|---|---|---|---|---|
| Prey type | 1 | 2 | 3 | 4 | Total |
| Field vole (*Microtus agrestis*) | 1 | 1 | 0 | 0 | 2 |
| *Microtus sp*. | 20 | 17 | 13 | 16 | 66 |
| Bank vole (*Myodes glareolus*) | 7 | 4 | 1 | 1 | 13 |
| Bank vole or *Microtus sp*. | 0 | 0 | 0 | 1 | 1 |
| Wood lemming (*Myopus schisticolor*) | 4 | 1 | 12 | 0 | 17 |
| Vole (Microtinae) | 7 | 2 | 1 | 6 | 16 |
| Birch mouse (*Sicista betulina*) | 5 | 0 | 0 | 0 | 5 |
| Rodent (Rodentia) | 1 | 0 | 0 | 0 | 1 |
| Shrew (*Sorex sp*.) | 5 | 0 | 6 | 39 | 50 |
| Small mammal | 0 | 0 | 1 | 0 | 1 |
| Song thrush (*Turdus philomelos*) | 0 | 1 | 0 | 0 | 1 |
| Warbler (Sylviidae) | 1 | 0 | 0 | 0 | 1 |
| Blue tit (*Cyanistes caeruleus*) | 1 | 0 | 0 | 0 | 1 |
| Bird nestling | 0 | 1 | 0 | 0 | 1 |
| Unidentified prey | 0 | 1 | 0 | 2 | 3 |
| Total | 52 | 28 | 34 | 65 | 179 |

The total mass of all the prey items was calculated to be 3995 g, with a mean body mass of 22.6 (95% CI 21.1, 24.1) g per prey item. *Microtus* voles accounted for more than half of the total mass (Table 3). In addition, shrews and wood lemming were important groups with about 12% of the total body mass each.

**Table 3:** Proportion (%), number and body mass for the different prey categories among prey delivered by Tengmalm's owl males at the nest. Field vole (*Microtus agrestis*) and *Microtus* voles are pooled, and the birds are pooled. Unidentified preys are omitted due to lack of body mass estimates.

| Prey category | Number of items | % of all prey items | Individual body mass (g) | Total body mass (g) | % of total estimated mass |
|---|---|---|---|---|---|
| *Microtus sp.* | 68 | 38.6 | 30 | 2040 | 51.1 |
| Bank vole (*Myodes glareolus*) | 13 | 7.4 | 20 | 260 | 6.5 |
| Bank vole or *Microtus sp*. | 1 | 0.6 | 25 | 25 | 0.6 |
| Wood lemming (*Myopus schisticolor*) | 17 | 9.6 | 30 | 510 | 12.6 |
| Vole (Microtinae) | 16 | 9.1 | 28.7 | 459.2 | 11.5 |
| Birch mouse (*Sicista betulina*) | 5 | 2.8 | 10 | 50 | 1.2 |
| Rodent (Rodentia) | 1 | 0.6 | 27.9 | 27.9 | 0.7 |
| Shrew (*Sorex sp.*) | 50 | 28.4 | 10 | 500 | 12.5 |
| Small mammal | 1 | 0.6 | 22.7 | 22.7 | 0.6 |
| Bird | 4 | 2.3 | 25[1] | 100 | 2.5 |
| Total | 176 | 100 | _ | 3994.8 | 99.8 |

[1] Mean estimate, variation 10-70 g (95% CI -22.7, 72.7)

The male at nest 4 had the highest delivery rate in terms of prey mass (Table 4), even though he had the lowest mean body mass per prey. The opposite applied for the male at nest 2; he had the highest mean prey body mass, but lowest prey delivery rate in terms of mass. The survival rate of the nestlings at nest 2, from start of filming until fledging, was only 40%, while it was a 100% at the other locations.

**Table 4:** Mean prey body mass and prey delivery rate at each Tengmalm's owl nest (Nest ID 1-4). Unidentified preys are omitted.

| Nest ID | Number of prey items | Total mass (g) | Mean body mass (±SE) per prey | Hours filmed | Mass delivered per hour filmed |
|---|---|---|---|---|---|
| 1 | 52 | 1238.8 | 23.8 (± 8.32) | 58.09 | 21.3 |
| 2 | 27 | 787.4 | 28.8 (± 9.73) | 38.52 | 20.4 |
| 3 | 34 | 881.4 | 25.9 (± 7.77) | 31.18 | 28.3 |
| 4 | 63 | 1087.2 | 17.2 (± 9.37) | 34.43 | 31.6 |

## 3.2 Factors influencing prey delivery

No factors contributed significantly to explain the delivery of a wood lemming or a shrew after I had controlled for the random effect of nest ID. For *Microtus* voles, there was a significant effect on the nestlings' age and the delivery of *Microtus*. The probability that the delivery prey item was a *Microtus* vole increased with the nestlings age (Table 5, Figure1). For bank vole there was a significant effect of date and whether or not the bank vole was delivered in the evening (before solar midnight) or in the morning (after solar midnight) (Table 6). The probability that a delivered prey was a bank vole was higher early in the season and decreased throughout June, and was higher after solar midnight then before solar midnight (Figure 2). Ambient temperature had no influence on the probability of delivering any specific prey type.

**Table 5:** Parameter estimates from a logistic multilevel regression model with the probability that a prey item delivered was a *Microtus* vole as response variable and nestling age as explanatory variable. (n=158). Nest ID is used as a random factor (n=4).

| | Estimate | SE | z-value | p |
|---|---|---|---|---|
| Intercept | -1.86 | 0.81 | -2.29 | 0.022 |
| Nestlings age | 0.09 | 0.04 | 2.40 | 0.016 |

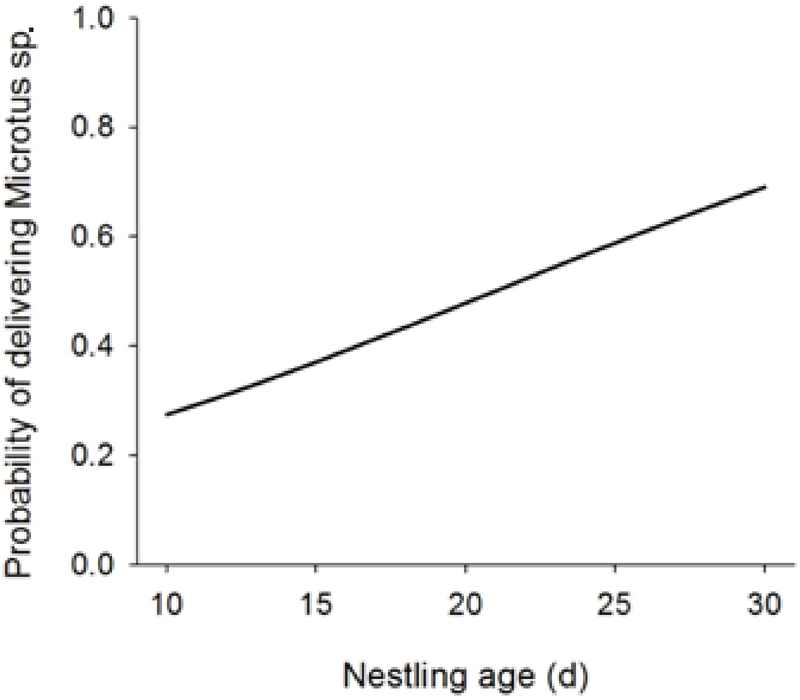

**Figure 1:** The probability that a prey item delivered at the nest was a *Microtus* vole as function of nestling age (days) (n=158). For data distribution see Appendix1.

**Table 6**: Parameter estimates from a logistic multilevel regression model with the probability that a prey item delivered was a bank vole as response variable, and whether the prey was delivered before or after solar midnight (SM), and the date of delivery as explanatory variables (n=157). Nest ID is used as a random factor (n=4).

| | Estimate | SE | z-value | p |
|---|---|---|---|---|
| Intercept | -0.29 | 0.58 | -0.50 | 0.62 |
| Before or after SM | 1.62 | 0.66 | 2.46 | 0.014 |
| Date | -0.10 | 0.04 | -2.75 | 0.0059 |

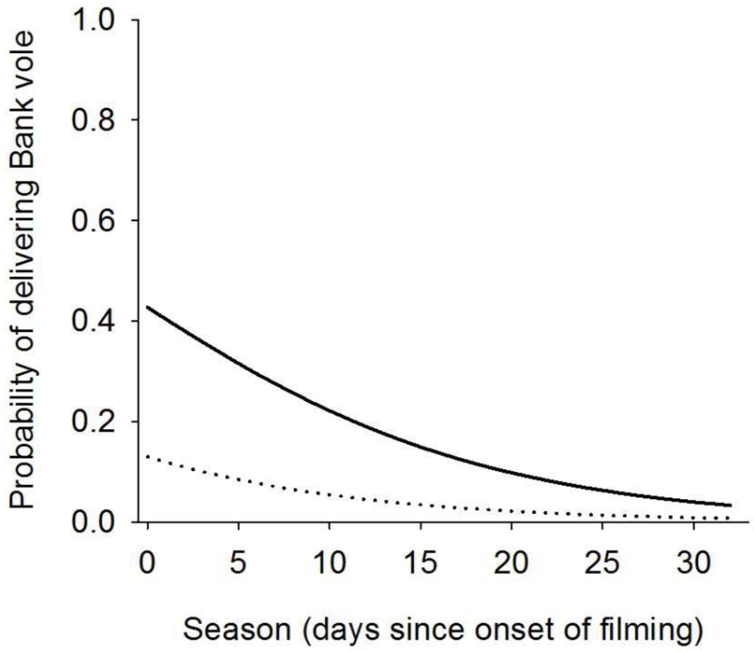

**Figure 2:** The probability that a bank vole was delivered in the evening (before solar midnight) (dotted line), or in the morning (after solar midnight) (solid line), as a function of season (number of days after 31. May) (n= 157). For data distribution see Appendix 2.

## 3.3 Win-stay or win-shift hunting strategy

To test if a win-stay or a win-shift hunting strategy was prominent in the male Tengmalm's owls, I tested which factors affected whether or not the delivered prey item was of the same species as the previous prey item delivered at the nest. In these nests, all prey items other than those identified as bank vole, *Microtus* vole, wood lemming or shrew were excluded. If the prey item delivered was the same species as the last one, and the time interval between those two was short, it would have indicated a win-stay hunting strategy.

A prey item delivered was more likely to be of the same species than of another species, significantly so for nest 4, marginally non-significantly for nest 2, and not significantly so for nests 1 and 3 (Figure 3).

The p-values from the likelihood-ratio estimator and the Pearson estimator was used in a meta-analysis, to test if there was a general tendency that the current prey item was the same as the previous when correcting for nest ID. Fischer´s combined probability test was used, and the tests were significant for the estimates from the linear regression analyses (p= 0.030), as well as for the Pearson estimates (P = 0.039), which states that there was a general significant tendency towards delivering prey items in runs after correcting for nest ID.

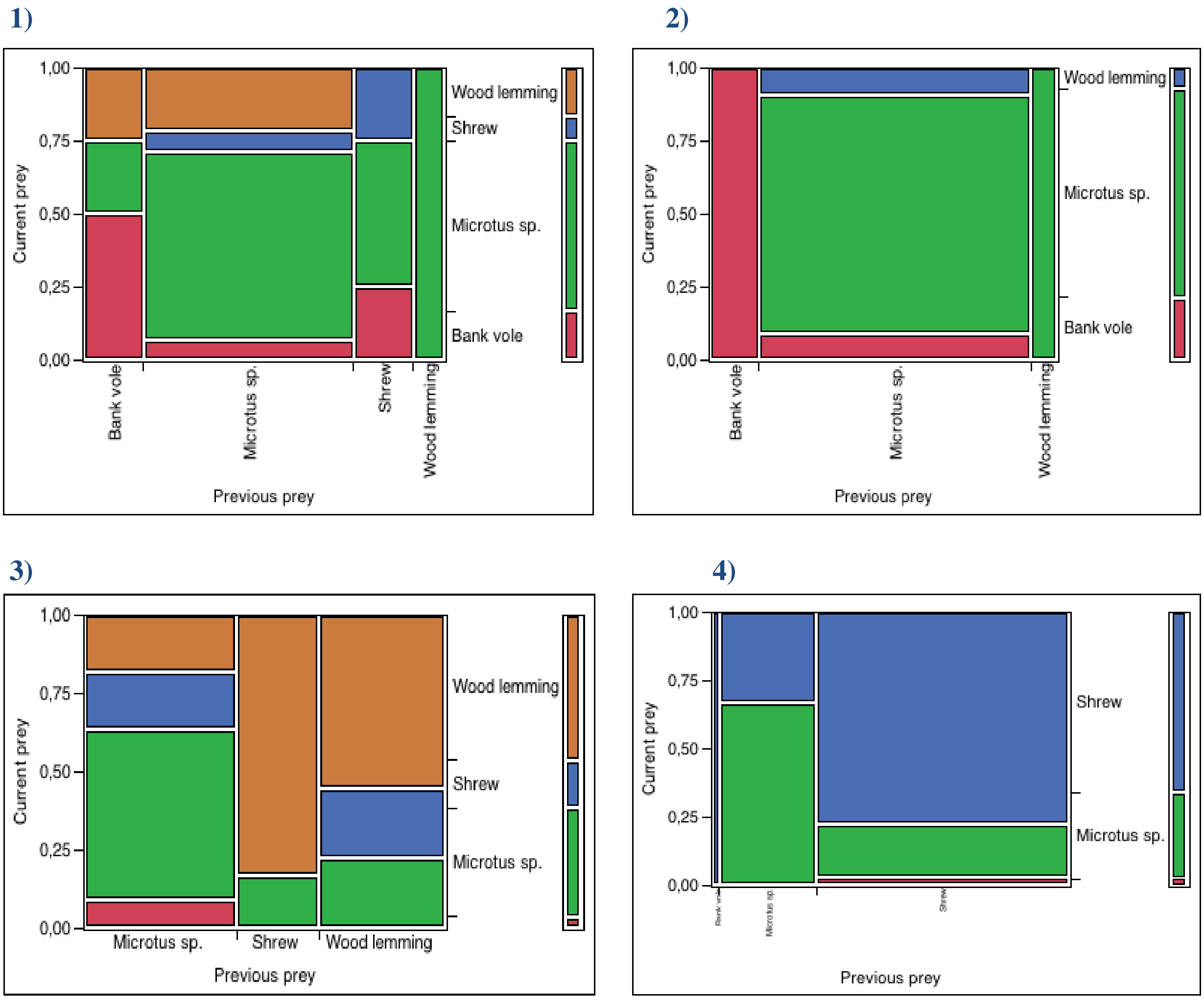

**Figure 3:** Mosaic plots illustrating the probability of a prey item delivered (current prey) was the same species as the previous (previous prey) for each prey group. Sample size (n) and p-values from the likelihood-ratio (LR) $\chi^2$ estimator and the Pearson $\chi^2$ estimator are given for each nest site (1-4): 1) n=24, LR p = 0.41, Pearson p = 0.47. 2) n=14, LR p= 0.090, Pearson p=0.068. 3) n=26, LR p=0.12, Pearson p=0.19. 4) n=44, LR p=0.046, Pearson p=0.049.

To test if the time elapsed between the two deliveries also was significant, a nominal logistic test was run with whether or not a prey item was of the same type as the previous delivered item as response variable. Explanatory variables were time since previous delivery, the prey category (bank vole, *Microtus* vole, wood lemming or shrew), and the interaction between those two. Nest ID was not corrected for because of uneven distributed data. The interaction was significant (p = 0.047), and after sorting out each prey category the probability of a shrew being delivered if the previous prey delivered was a shrew declined with increasing time elapsed between the two deliveries (Table 7, Figure 4), as expected in a win-stay hunting strategy. The test was not significant for any other prey types.

**Table 7:** Parameter estimates from a logistic regression analyses of the probability that a prey item delivered would be a shrew if the last one was a shrew, as a function of time since the previous shrew was delivered (n=42).

| | Estimate | SE | Chi-square | p |
|---|---|---|---|---|
| Intercept | 1.54 | 0.64 | 5.85 | 0.016 |
| Time since last delivery | -0.001 | 0.0004 | 4.06 | 0.044 |

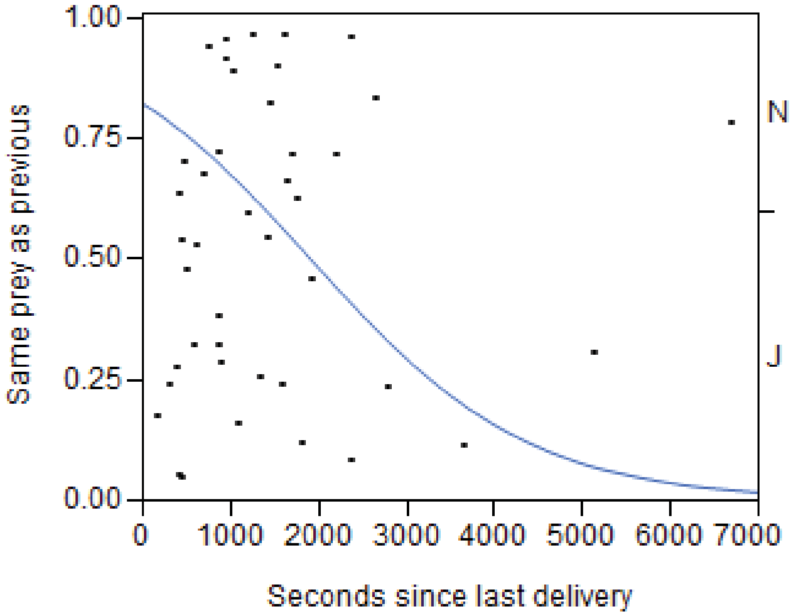

**Figure 4:** The probability that an item delivered at the nest was a shrew if the previous item was a shrew decreased with time elapsed since previous delivery (n=42). J = A prey item delivered was a shrew, N = A prey item delivered was not a shrew.

## 3.4 Prey handling

Among the 179 prey items, 25 were decapitated before being delivered by the male at the nest, and 23 of those were voles, which is 19% of all identified voles. Among the decapitated prey items were 21 *Microtus* voles, amounting to 34% of all delivered *Microtus* voles. One shrew and one unidentified prey item were also decapitated. It is uncertain whether or not the birds where decapitated, as essential body parts were hidden from the camera during delivery, and later underneath the nestlings.

To find out which factors that might influence whether or not a prey item was decapitated, I ran a logistic multilevel regression with decapitation of a prey as response variable and different time measures as explanatory variables. In the test where time variables were delivery time, taken as the number of minutes elapsed from 0800 p.m., and delivery time squared, the test was clearly unstable and therefore discarded. Another test was run with other time measures as explanatory variables (Table 8). In this test, there was a significant effect of prey body mass and minutes since solar midnight (SM). Larger prey were more often decapitated than the small ones and the probability of decapitation increased from SM (Figure 5). Out of 25 decapitated prey items 24 was decapitated before SM (Appendix 3).

The probability of delivering a decapitated prey differed between the nests, with only one decapitated prey at nest site 4, out of 58 prey items (0.02%), while nest site 2 had the most with nine out of 16 prey items decapitated (36%).

**Table 8:** Parameter estimates from a logistic multilevel regression model with the probability that a prey item was decapitated prior to delivery at the nest as response variable. Prey body mass and minutes since solar midnight (SM) was used as explanatory variable (n= 160). Nest ID is random factor (n=4).

| | Estimate | SE | z-value | p |
|---|---:|---:|---:|---:|
| Intercept | -6.39 | 1.53 | -4.18 | < 0.0001 |
| Minutes since SM | 0.016 | 0.0058 | 2.79 | 0.0052 |
| Prey body mass | 0.13 | 0.049 | 2.57 | 0.010 |

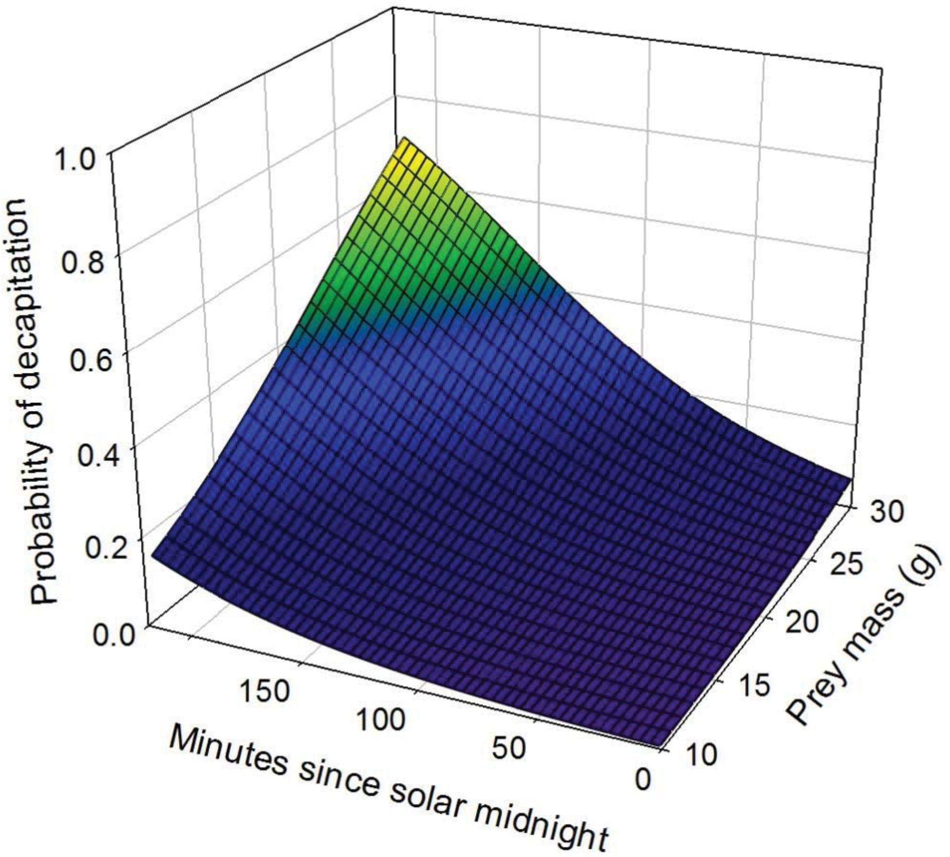

**Figure 5:** The probability that a prey item was decapitated prior to delivery at the nest increased with minutes since solar midnight and size of the prey (n=160). For data distribution see Appendix 4.

## 3.5 Feeding behavior

As the nestlings became older, they started to handle and consume prey on their own as their swallow capacity increased. Of the 179 prey items delivered at the nest, handling behavior was recorded for 148. The female handled 68 prey items, and the nestlings 80. There was a shift in feeding behavior when the nestlings were about 18 days old (Figure 6). At that age they started to handle and consume their prey unassisted, were before the female had plucked the prey. The only significant explanatory variable for whether the female or the nestlings handled the prey was the age of the oldest nestling at the time of delivery (Table 9). The body mass of the prey had no significant effect on who handled the prey.

**Table 9:** Logistic regression model of the probability that the female fed the nestlings rather than the nestlings fed unassisted as response variable, and age of the oldest nestling and prey body mass as explanatory variables (n=146). Nest ID is used as random factor (n=4).

| | Estimate | SE | z-value | p |
|---|---|---|---|---|
| Intercept | -12.53 | 2.56 | -4.89 | <0.0001 |
| Nestlings age | 0.75 | 0.15 | 5.07 | <0.0001 |
| Prey body mass | -0.044 | 0.035 | -1.27 | 0.21 |

The task of handling the prey shifted from female to nestlings when they were 18.5 days old (95% CI 17.7, 19.4). In the middle stage both the female and the nestlings were handling the prey until all the nestlings were old enough to eat independently.

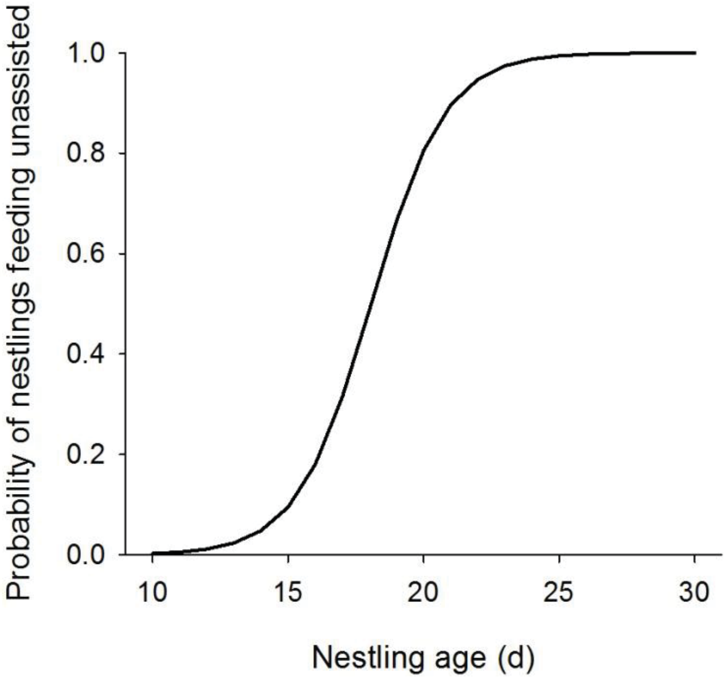

**Figure 6:** The probability that the prey item was handled by the female or the nestlings. The main handler shifted from female to nestlings when the nestlings were about 18 days old (n=146). For data distribution see Appendix 5.

# 4.0 Discussion

## 4.1 Prey delivery at the nest

*Microtus* voles were most abundant prey with 39% of prey number delivered and 51% of the delivered prey mass. Bank vole represented 7% of the prey items and 7 % of the body mass, while wood lemming amounted 10% of the prey number and 13% of the prey mass, respectively. Shrews accounted for 28% of the prey items and 13% of total prey mass, but 39 of 50 specimens where delivered at one nest, making shrew an infrequent prey in the other nests, and totally absent at one. Only four birds were recorded delivered, two on each of two nests.

Voles made up more than 90% of the diet of Tengmalm's owl during the breeding seasons of 1980–1986 in northern Sweden (Hörnfeldt et al. 1990), and the availability of prey is expected to have a positive effect on the delivery rates in Tengmalm's owl (Zárybnická et al. 2012). Korpimäki (1988) also found that *Microtus* voles where the most abundant prey group in the caches of Tengmalm's owl (Korpimäki 1988). Abundance of *Microtus* voles is the most important factor determining the diet composition of breeding Tengmalm's owls (Korpimäki & Norrdahl 1989), and *Microtus* voles is assumed to be the most profitable prey (Jacobsen & Sonerud 1993).When voles are scarce, Tengmalm's owl change diet towards shrews and passerine birds as most important prey, with birds representing as much as half of the total body mass in the owls diet in low vole years (Hakkarainen et al. 1997; Korpimäki 1988; Korpimäki & Norrdahl 1989). My study was conducted in a year of increasing vole abundance in the fairly predictable 3-4-year population cycle (Hakkarainen et al. 1997) and Tengmalm's owls is known to show rapid functional response to changes in vole densities (Korpimäki & Norrdahl 1989). The increasing availability of voles in my study area might therefore explain the large proportion of voles in the owl's diet, and the few deliveries of shrews (with exception of one nest) and birds.

When comparing the trapping indexes from Hamar and Elverum, bank vole had the highest abundance at both locations, followed by *Microtus* voles (*Microtus agrestis*) in Hamar, and wood lemming in Elverum, making voles the most abundant prey in the field as well as in the owls' diet.

## 4.2 Factors influencing prey delivery

I found that among the delivered prey items there were more bank voles early in the season and *Microtus* voles late in the season. In an increase phase of the vole cycle, the vole abundance is moderate in spring, but is expected to increase throughout the summer towards a peak in the next autumn (Korpimäki & Hakkarainen 1991). Studies on diet and habitat use have shown a snow dependent diet switch in Tengmalm's owl (Hörnfeldt et al. 1990; Jacobsen & Sonerud 1993; Sonerud 1986), where bank vole predominated the diet early in the season during laying, when snow covered the ground (Hörnfeldt et al. 1990). Tengmalm's owls primarily use forest as hunting grounds during this period (Jacobsen & Sonerud 1993). When the snow melted, the owl changed hunting habitat and diet as a response to higher availability of *Microtus* voles in the clear cuts (Jacobsen & Sonerud 1993). These diet shifts can explain why more bank voles was delivered early in the season, and more *Microtus* as the nestlings grew older.

This diet shift might also have caused an overestimation of *Microtus* voles in the diet in my study, as the diet could have contained a larger proportion of bank voles earlier in the season; before I began video monitoring at the nests. *Microtus* voles are the heaviest and probably the most profitable prey for Tengmalm's owl (Jacobsen & Sonerud 1993), they are also known to be slow and clumsy, and thereby easier to catch when encountered compared to the agile bank vole (Hansson 1987; Jacobsen & Sonerud 1993). Jacobsen &Sonerud (1993) found that when the vegetation cover in the clear cuts became denser during the season, the *Microtus* voles were less available and the owl showed a tendency to switch back to forest again, resulting in more bank voles in the diet (Jacobsen & Sonerud 1993; Sonerud 1986). No such patterns was evident in my results, but since I stopped recording in early July a second habitat shift might have occurred later.

All the nesting pairs in my study were successful, with four fledglings and no mortality at nest sites 1, 3 and 4, and two fledglings and 60% mortality at nest site 2. Other studies have found that fledglings per pair increases with the abundance of *Microtus* voles (Korpimäki & Norrdahl 1989). Nestlings raised in the increase phase are expected to have twice the chance of surviving their first winter compared to those reared in the other phases, because the yearling survival is determined largely by the vole supply (Korpimäki & Hakkarainen 1991).

The Tengmalm's owls at nest site 1 had the earliest clutch out of the four. Hakkarainen (2003) found that owls in territories with larger areas of agricultural land tended to produce earlier clutches in increasing vole years compared to owls in habitats  predominated by other features (Hakkarainen et al. 2003). This fits well with my study, where nest site 1 had one of the largest proportions of agricultural land in the home range, and was also using it most actively (Sørås 2014). This pattern is probably connected to the abundance of *Microtus* voles, which occupy open habitat like clear cuts and agricultural land. Those habitat types have low vegetation cover in the spring which make the voles more exposed to avian predators and thereby becomes easy targets (Korpimäki & Norrdahl 1989). Bank voles on the other hand  is most common in woodland, while shrew occurs in both habitats, but prefers productive areas (Korpimäki & Norrdahl 1989). When assessing the owls home range, the productivity proved to be much higher in Elverum, at nest 4 (Sørås 2014) compared to other nest sites, which also might explain the large proportion of shrews at that particular nest.

The Tengmalm's owls in my study tended to deliver bank voles in the morning, rather than the evening. Studies done on central place foraging single prey loaders have shown that avian predators carries larger prey to the nest while consuming smaller prey (with a threshold value of c.10% of the predators body mass) at the capture site, which should be the most energy efficient behavior (Sonerud 1989). This is known as the load size effect(Sonerud 1989, 1992). Many studies, including mine, have based their diet analyses on the prey delivered at the nest site. The danger of overestimating the proportion of larger prey and underestimating smaller ones may therefore be prominent (Sonerud 1992). As *Microtus* voles and wood lemming are the largest prey with approximately 30 g each, they might have been overestimated in the diet compared to bank voles (20 g) and shrews (10 g). The male Tengmalm's owl have a body mass of approximately 100 g suggesting that shrews are most likely to be eaten at the capture site, with a body mass of approximately 10% of the Tengmalm's owls body mass. Bank voles might also be eaten at the capture site if shrews are scarce in the field. I therefore suggest that the load size effect might explain why bank voles were more often delivered in the morning hours (after solar midnight) than other prey types. If the male consume the smallest prey items in the evening because of hunger after a day on roost, he might become satiated during the night and consequently deliver all the prey items caught in the morning hours at the nest. I suspected that the bank voles daily activity rhythm also might have influenced my findings, but Buchalczyk (1964) found that bank voles had activity peaks around 10 p.m. and 06 a.m. which does not explain my results (Buchalczyk 1964) . However, the study was conducted in Poland, and voles in northern Europe might have another activity rhythm than in central Europe that could explain why bank voles tended to be caught in the morning (Zárybnická et al. 2012). My sample size of bank voles is scarce, so a larger sample might have resulted in other delivery patterns.

My results showed that the male at nest 4 had the highest total prey mass delivered, even though he had the lowest mean mass per prey item delivered. This might show a tendency for the male to compensate for the small prey load by more frequent deliveries at the nest. Studies have shown that the males adjust their delivery rate with nestling requirements, and increase delivery rates both in terms of prey number and prey mass with higher demand (Zárybnická et al. 2012).The opposite applied for the male at nest 2; he had the highest mean prey body mass, but the lowest rate of prey mass delivered. This might have caused the low nestling survival in this nest.

### 4.3 Win-stay or win-shift hunting strategy

My results showed that the male Tengmalm's owls had an overall tendency of catching prey items in runs, as prominent in a win-stay hunting strategy. However, the pattern differed between the prey types. Whereas the probability of a shrew being delivered if the previous prey delivered was a shrew declined with increasing time elapsed between the two deliveries. There was no such effect for the other prey-types. Because of this, only one criteria is fulfilled, and my results does not have the necessary support to state that Tengmalm's owl males uses a win-stay hunting strategy. To achieve that, I would also need information about the male Tengmalm's owl's movements in the field.

A win-stay hunting strategy on small mammals has been found in other species, including kestrel (*Falco tinnunculus*), hawk owl (*Surnia ulula*) and ferruginous hawk (*Buteo regalis*) (Sonerud 1985b). Tengmalm's owl has been observed to return to the nest with small bird nestlings, one at a time, clearly returning to the same hunting site (Norberg 1970). This is evidently a use of the win-stay hunting strategy. Voles are distributed unequally in the habitat, making some hunting sites better than others depending on prey type. According to Sonerud (1985b) the most successful strategy in that situation would be to return to a successful hunting site rather than search at random, based on the theory that the predator possesses a well developed topographic memory. A nesting Tengmalm's owl is a central place forager as it departs from and returns to a central place, the nest (Andersson 1981). Species with this behavior will have a higher energy cost when hunting far from the central place, and therefore do well if it returns to a successful hunting site nearby the central place. Foraging behavior is under strong selection for efficiency (Andersson 1981), and when confronted with prey items of various degree of clumped or stationary distribution, an area-concentrated search has proven to be the most successful one (Sonerud 1985b). Tengmalm's owl has probably thereby developed a strategy with successive returns to the clump from a central place, called the win-stay strategy (Sonerud 1985b).

## 4.4 Prey handling

My results showed that the probability of decapitation increased with the body mass of the prey item. Steen et al. 2010 found the same pattern for the Eurasian kestrel, and explained it by the feeding constraint hypothesis, which states that the nestling's inability to ingest larger prey items affects the evolution of parental behavior. The extent of prey preparation should thereby increase with prey size and decrease with nestling age (Steen et al. 2010). Prey preparation is here understood as decapitation, or other forms of prey handling, either done by the food providing parent before delivery at the nest, often the male, or plucking of prey at the nest, done by the female. The probability of decapitating prey items did not decrease with nestlings age in my study, but it increased with prey size, which might be explained by the nestlings gape size limit and swallowing capacity, as argued by Steen et al. (2010). The digestion of bones and skulls might be less efficient in young nestlings (Steen et al. 2010), and decapitation of prey prior to delivery may therefore increase the ingestion rate of the prey item, leaving the female and nestlings with more time to feed and brood (Rands et al. 2000; Slagsvold & Sonerud 2007). Decapitation of the heaviest prey items may also decrease the load carried back to the nest, without decreasing the digestible prey biomass delivered (Sodhi 1992; Steen et al. 2010). Sodhi (1992) and Rands et al. (2000) also suggested that the energy used on transport might be less if the prey is decapitated before departure from the capture site, making it more aerodynamic (Rands et al. 2000; Sodhi 1992). The head of the prey may cause wind resistance when carrying avian prey, but the effect is less essential when carrying voles (Steen et al. 2010), making it unlikely the only reason explaining decapitation of prey by male Tengmalm's owl.

The probability of decapitation increased with minutes since solar midnight, with a tendency of decapitating the prey items before solar midnight rather than after. I have not found any studies detecting this pattern before, but it fits the proposal by Rands et al. (2000), that consuming removed prey parts would reduce the time needed for self-foraging and thereby increase overall delivery rate (Rands et al. 2000). I therefore suggest that hunger after a day on roost causes the male to decapitate suitable prey items until he is satiated, delivering whole prey items at the nest until he possibly turns hungry again, explaining why fewest prey items were decapitated in the darkest part of the night. This is probably a supplement to smaller prey items, eaten at the capture site, and therefore not recorded at the nest.

The probability of delivering a decapitated prey differed between the breeding pairs, with only one decapitated prey at nest site 4, and 16 decapitated prey at nest site 2. Mean prey body mass was highest at nest site 2, and lowest at nest site 4 which might explain the large differences between the nests, as the Tengmalm's owl significantly tended to decapitate larger prey items.

There was a non-significant tendency of lower probability of decapitation with increasing nestling age. I suspect that this effect could have been significant if the sample size was larger and video monitoring had started earlier. The youngest nestling filmed (oldest in the brood) where 10 days old at the onset of filming. The probability of decapitation might have been higher before I started filming, when the nestlings was younger, and then decreased with the nestlings age.

Nonetheless, my results suggest that decapitation of prey in Tengmalm's owl not necessarily is a part of prey preparation for the nestlings as a result of gape size limitations or swallowing capacity, but rather a trait developed by the providing parent to increase its delivery rate at the same time as its need for self-feeding is met, and without decreasing the digestible prey body mass delivered at the nest (Sodhi 1992).

## 4.5 Feeding behavior

I found that the probability of the nestlings handling the prey unassisted increased with the nestlings' age. This was as predicted and was also found in earlier studies (Sonerud et al. 2014). Prey body mass is expected to have an impact on whether the female is the prey handler, as gape size limits the nestlings swallowing capacity. The female is therefore expected to handle larger prey for a longer time period than small prey items, as the nestlings need to be older in order to swallow them whole (Sonerud et al. 2014; Steen et al. 2010). In my study prey body mass did not affect the probability of the nestlings feeding unassisted, but handling time is expected to increase with prey body mass (Sonerud et al. 2014). This suggests that the nestlings would be able to feed unassisted at an earlier stage if smaller prey items were delivered, and also relieve the female from prey partitioning (Sonerud et al. 2014). In my study the nestlings were about 18 days old when they started to pluck their own prey or swallowing it whole. This is approximately the same age as Sonerud et al. (2014) found in their study. The first prey items swallowed were shrews (personal observation), which demand less gape size than the larger voles. As their swallowing capacity increased and their beak developed, the nestlings were able to handle all prey items unassisted.

## 4.6 Conclusion

*Microtus* voles were the most common prey type delivered by the Tengmalm's owls in my study. My results suggest that the capture rate of *Microtus* voles increased during the season as the nestlings grew older, which may be explained by a diet switch from bank voles to *Microtus* voles when *Microtus* voles are more available in the field. My results showed that the owls delivered prey items in runs, as prominent in a win-stay hunting strategy which is believed to be the most energy efficient strategy while hunting voles. This supports earlier studies. The probability of decapitation of prey before delivery at the nest increased with time since solar midnight and the body mass of the prey, but was not affected by nestling age. This might indicate an efficient foraging behavior in the male, which decreases the time spent on self-foraging, and thereby increases the number of deliveries at the nest.

Video monitoring at the nest has proven to be a successful way of assessing the Tengmalm's owl's diet and feeding behavior. However, further studies should be supplied by behavioral data from the male hunting, as prey load effects and prey handling outside the nest may cause incorrect estimates of the quantities and significance of the different prey species in the diet.

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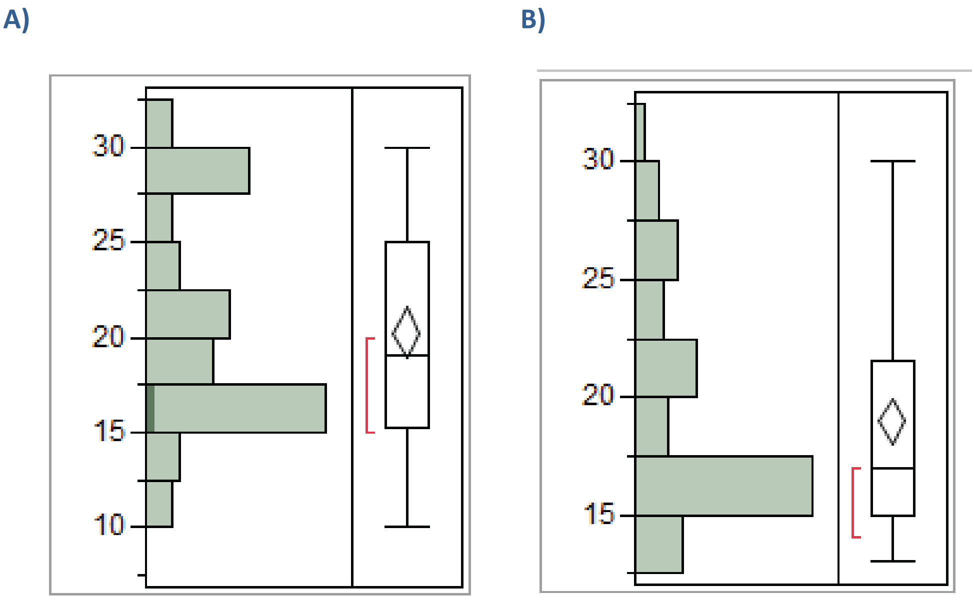
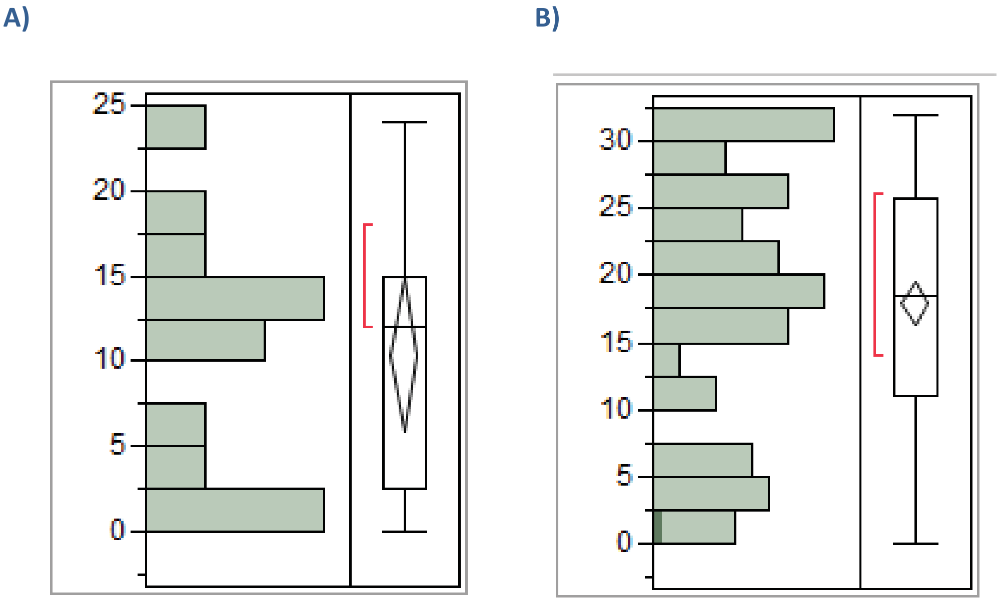
# 6.0 Appendix

**Appendix 1:** Distribution of my raw data material as illustrated by JMP. A) Delivery of *Microtus* at nest distributed on nestling age (days). B) Delivery of other prey types at nest distributed on nestling age. Mean, standard deviation, standard error and confidence interval is given in the table below.



| Summary statistics | Delivery of *Microtus* | Not *Microtus* |
|---|---:|---:|
| Mean | 20.25 | 18.99 |
| Std Dev | 5.72 | 4.64 |
| Std Err Mean | 0.69 | 0.49 |
| Upper 95% Mean | 21.63 | 19.96 |
| Lower 95% Mean | 18.87 | 18.01 |
| N | 68 | 90 |

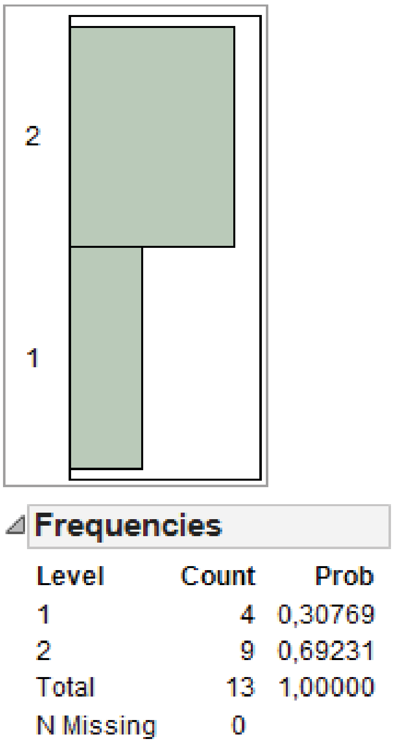
**Appendix 2:** Distribution of my raw data as illustrated by JMP. A) Delivery of bank vole at nest distributed on date of the delivery (taken from 31 May). B) Delivery of other prey types at nest distributed on date of the delivery. Mean, standard deviation, standard error and confidence interval is given in the table below.



| Summary statistics | Delivery of bank vole | Not bank vole |
|---|---:|---:|
| Mean | 10.38 | 17.90 |
| Std Dev | 7.54 | 9.55 |
| Std Err Mean | 2.09 | 0.80 |
| Upper 95% Mean | 14.94 | 19.48 |
| Lower 95% Mean | 5.83 | 16.33 |
| N | 13 | 144 |

Distribution of my raw data as illustrated by JMP. A) The amount of bank voles delivered in the evening (1) or in the morning (2). B) Delivery of other prey type in the evening (1) or in the morning (2). Estimates are given in the tables below.

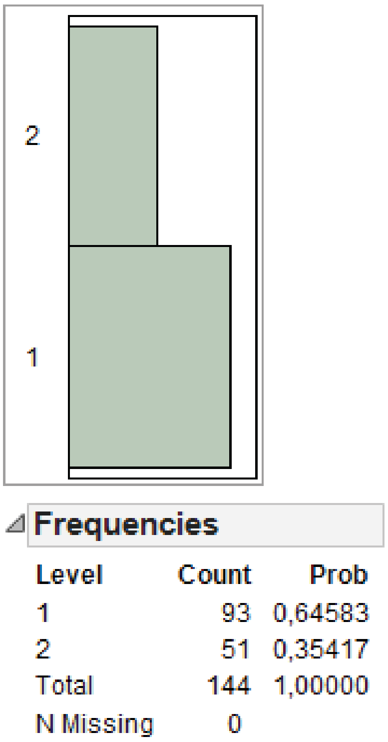
**A)**



**Frequencies**

| Level | Count | Prob |
|---|---|---|
| 1 | 4 | 0,30769 |
| 2 | 9 | 0,69231 |
| Total | 13 | 1,00000 |
| N Missing | 0 | |

**B)**

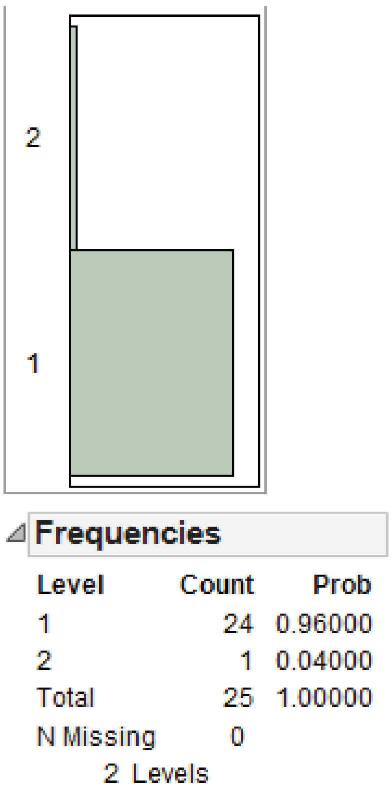


**Frequencies**

| Level | Count | Prob |
|---|---|---|
| 1 | 93 | 0,64583 |
| 2 | 51 | 0,35417 |
| Total | 144 | 1,00000 |
| N Missing | 0 | |

**Appendix 3:** Distribution of my raw data as illustrated by JMP. A) The amount of decapitated prey items delivered in the evening (1) or in the morning (2). B) Delivery of non-decapitated prey items in the evening (1) or in the morning (2). Estimates are given in the tables below.

**A)**

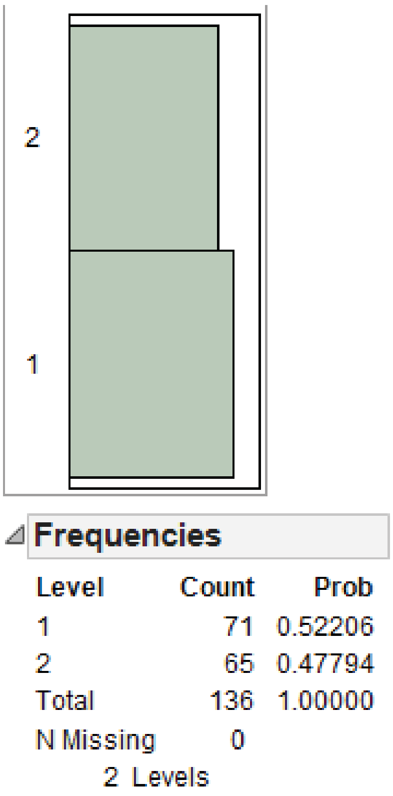


**Frequencies**

| Level | Count | Prob |
|---|---|---|
| 1 | 24 | 0.96000 |
| 2 | 1 | 0.04000 |
| Total | 25 | 1.00000 |
| N Missing | 0 | |

2 Levels

**B)**

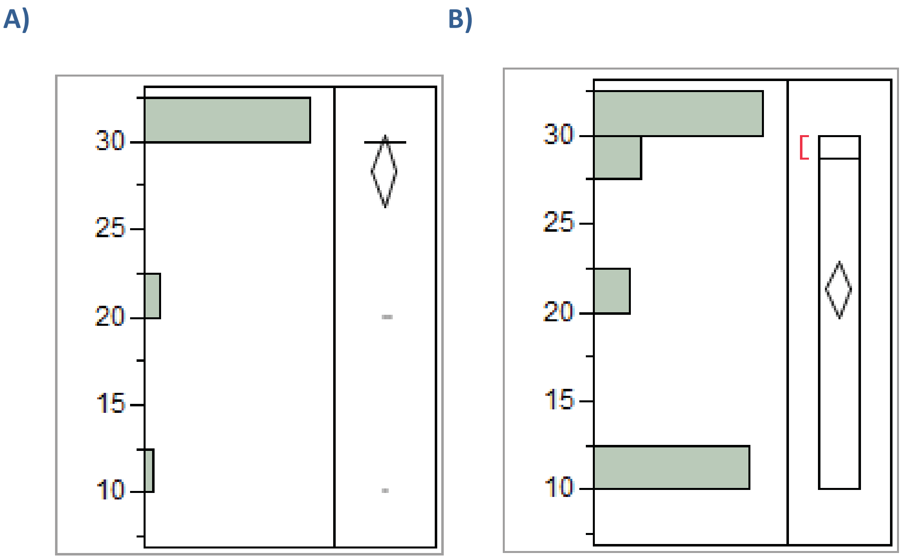


**Frequencies**

| Level | Count | Prob |
|---|---|---|
| 1 | 71 | 0.52206 |
| 2 | 65 | 0.47794 |
| Total | 136 | 1.00000 |
| N Missing | 0 | |

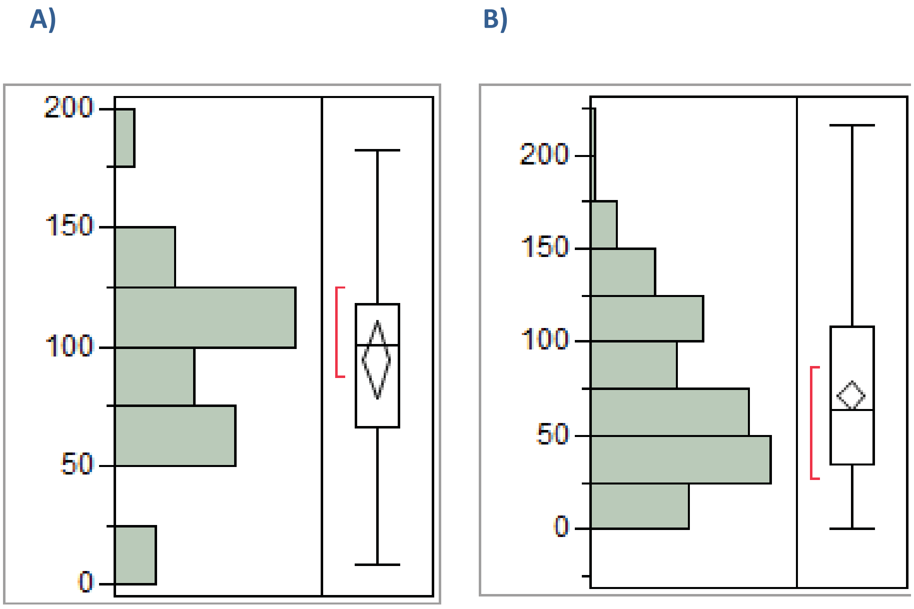
2 Levels

**Appendix 4:** Distribution of my raw data as illustrated by JMP. A) Delivery of decapitated prey at nest distributed on prey body mass. B) Delivery of non-decapitated prey items at nest, distributed on prey body mass. Mean, standard deviation, standard error and confidence interval is given in the table below.



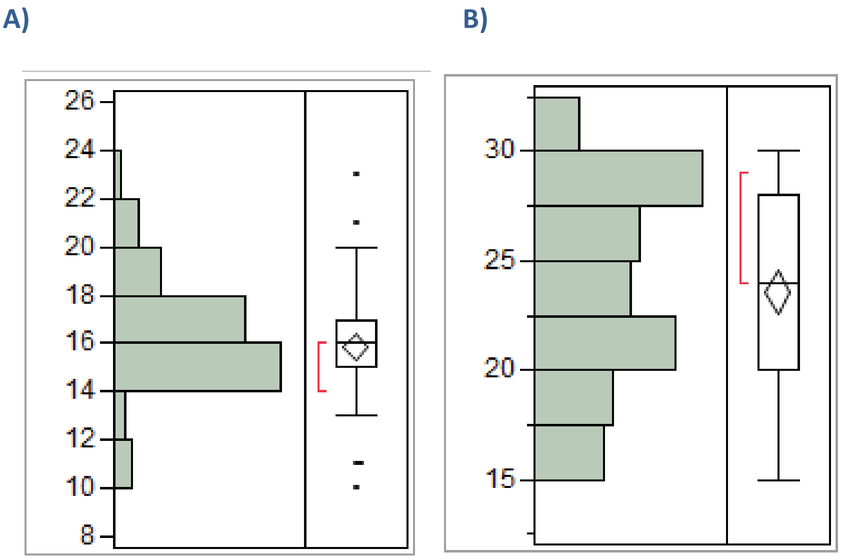
| Summary statistics | Decapitated | Not Decapitated |
|---|---:|---:|
| Mean | 28.33 | 21.31 |
| Std Dev | 4.81 | 9.33 |
| Std Err Mean | 0.98 | 0.80 |
| Upper 95% Mean | 30.37 | 22.90 |
| Lower 95% Mean | 26.30 | 19.72 |
| N | 24 | 136 |

Distribution of my raw data as illustrated by JMP. A) Delivery of decapitated prey at the nest, distributed on minutes since solar midnight (SM). B) Delivery of non-decapitated prey items at the nest, distributed minutes since SM. Mean, standard deviation, standard error and confidence interval is given in the table below.



| Summary statistics | Decapitated | Not Decapitated |
|---|---:|---:|
| Mean | 94.73 | 71.43 |
| Std Dev | 38.88 | 45.44 |
| Std Err Mean | 7.77 | 3.90 |
| Upper 95% Mean | 110.79 | 79.14 |
| Lower 95% Mean | 78.70 | 63.73 |
| N | 25 | 136 |

**Appendix 5:** Distribution of my raw data as illustrated by JMP. A) Prey items handled by the female, distributed on nestlings age. B) Prey items handled by the nestlings, distributed on nestlings age. Mean, standard deviation, standard error and confidence interval is given in the table below.



| Summary statistics | Handled by female | Handled by nestlings |
|---|---|---|
| Mean | 15.87 | 23.58 |
| Std Dev | 2.26 | 4.50 |
| Std Err Mean | 0.27 | 0.50 |
| Upper 95% Mean | 16.41 | 24.58 |
| Lower 95% Mean | 15.32 | 22.57 |
| N | 68 | 80 |

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