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Breeding and foraging strategies of Tengmalm's Owl
(*Aegolius funereus*) population in temperate area

(Hnízdní a potravní strategie středoevropské populace sýce rousného)

Dissertation thesis

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Prohlašuji, že jsem dizertační práci vypracoval samostatně s využitím uvedených literárních pramenů.

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3 Structure of the thesis

This Ph.D. thesis presents a syntax consisting of two different sources:

- The basis of the thesis forms the data from yet unpublished results about Tengmalm's owl diet and its relation to a changing abundance of their prey, including effects on reproductive success.
- The second part of the thesis introduces the published articles related to the topic of my Ph.D. thesis, on which I participated. One of six papers is included in Introduction chapter (Zárybnická et al. 2015b), one is introduced in Methods chapter (Zárybnická et al. 2016), one is used in Results chapter (Šindelář et al. 2015) and the other three papers are discussed in the Discussion chapter (Kouba et al. 2016; Zárybnická et al. 2017a; Ševčík et al. 2019).

The articles are following:

Šindelář, J., Kubizňák, P. & Zárybnická, M. 2015: Sequential polyandry in female Tengmalm's owl (*Aegolius funereus*) during a poor rodent year. *Folia Zoologica* 64 (2): 123-128. IF = 0.76.

Zárybnická, M., Riegert, J., Brejšková, L., **Šindelář, J.**, Kouba, M., Hanel, J., Popelková, A., Menclová, P., Tomášek, V. & Šťastný, K. 2015: Factors Affecting Growth of Tengmalm's Owl (*Aegolius funereus*) Nestlings: Prey Abundance, Sex and Hatching Order. *PLoS ONE* 10 (10): e0138177. IF = 3.54.

Zárybnická, M., Kubizňák, P., **Šindelář, J.** & Hlaváč, V. 2016: Smart nest box: a tool and methodology for monitoring of cavity-dwelling animals. *Methods in Ecology and Evolution* 7: 483-492. IF = 3.79.

Zárybnická, M., Riegert, J., Bejček, V., Sedláček, F., Šťastný, K., **Šindelář, J.**, Heroldová, M., Vilímová, J. & Zima, J. 2017: Long-term changes of small mammal communities in heterogenous landscapes of Central Europe. *European Journal of Wildlife Research* 63: 89. IF = 1.14.

Kouba, M., Bartoš, L., **Šindelář, J.** & Šťastný, K. 2017: Alloparental care and adoption in Tengmalm's Owl (*Aegolius funereus*). *Journal of Ornithology* 158 (1): 185-191. IF = 1.89.

Ševčík, R., Riegert, J., **Šindelář, J.** & Zárybnická, M. 2019: Vocal activity of the Central European Boreal Owl population in relation to varying environmental condition. *Ornis Fennica* 96: 1-19. IF = 0.56.

All articles are in complete form attached in the appendix.

4 Abstract

The effects of food abundance on Tengmalm's owl diet and reproductive success were examined in this thesis. The small mammal abundance based on regular field trappings was confronted with a composition of Tengmalm's owl diet. The diet structure was determined from video recordings made by innovative Smart nest boxes. The data (6392 male arrivals with prey) on nest monitoring were collected from brooding to the fledging period at 48 nests in four seasons (2014 – 2017) in the Ore Mountains, Czech Republic. Significant differences in among-year structure and abundance of small mammals were found. Within-year prey abundance was more stable, no dramatic changes occurred. Out of the Tengmalm's owl diet, only *Apodemus* mice corresponded with the structure of the food supply, with recognizable inclination to prey just on *Apodemus* mice. This result confirmed the importance of *Apodemus* mice in owl diet in Central Europe; the increased proportion of *Apodemus* mice in the diet resulted in increased clutch sizes, greater reproductive success (i.e. the total number of fledglings). *Microtus* voles also comprised the important part of Tengmalm's owl diet, but no significant positive correlation with fledgling production was found. Other types of mammal prey as *Sorex* shrews or *Myodes* voles were complementary and did not substitute main prey. Avian prey was only taken as an alternative prey and the higher proportion of birds in the diet decreased the reproductive output. Approximately 10-20% of Tengmalm's owl males use polygyny and cca 3% of females use sequential polyandry to increase their fitness, which occurs mostly in the food-rich season. However, female sequential breeding was once recorded even in the low-vole season and both nestings succeeded regardless. The anticipated negative effect of breeding at a later stage of the season on the number of fledglings was not confirmed, except for the food-rich year 2017. My findings document that the Central-European population of Tengmalm's owls deal with a different structure and population dynamics of small mammal communities than conspecifics from Fennoscandia, and therefore have evolved a little different strategy in dietary behaviour ensuring the most reproductive output possible.

5 Anotace

Tato práce má za cíl popsat vliv potravní nabídky na potravu sýce rousného a jeho reprodukční úspěšnost. Početnost drobných savců, stanovená na základě pravidelných odchytů, byla porovnána se složením potravy sýce rousného. Zjištění struktury potravy bylo prováděno za pomoci speciálních kamerových budek, tzv. “Smart nest boxes”. Tyto videonahrávky (celkem 6392 příletů samce s kořistí) z celého období hnízdění, tj. od inkubace po vylétnutí z hnízda, byly pořízeny na 48 hnízdech během čtyř sezón (2014 - 2017) v Krušných horách. Byly zjištěny podstatné meziroční rozdíly v početnosti jednotlivých druhů drobných savců. Vnitrosezónní fluktuace početnosti byly značně menší. Struktura potravy sýce rousného do značné míry korespondovala s potravní nabídkou, avšak byla zde patrná preference k lovu myšic rodu *Apodemus*. Takový výsledek potvrzuje důležitost myšice pro sýce ve střední Evropě; větší podíl myšic v potravě znamenal větší snůšky a vyšší reprodukční úspěšnost (tj. vyšší počet vylétlých mlád'at) sýce rousného. Hraboši rodu *Microtus* také tvořili podstatnou část potravy sýce, ovšem bez prokazatelného vlivu na produkci mlád'at. Ostatní druhy kořisti jako rejsci rodu *Sorex* nebo norník rudý *Myodes glareolus* sloužili v zásadě jako doplňková kořist a nedokázaly nahradit primární druhy kořisti. Ptáci byli přinášeni také jako doplňková kořist a podíl ptáků v potravě negativně koreloval s počtem vylétlých mlád'at. Zhruba 10 – 20 % samců využívá polygamii a okolo 3 % samic sukcesivní polyandrii ke zvýšení své reprodukční úspěšnosti, zejména během potravně bohatých sezón. Nicméně bylo zaznamenáno jedno hnízdění samice za použití strategie sukcesivní polyandrie. Přestože daná sezóna byla potravně chudá, obě hnízdění byla úspěšná. Očekávaný negativní dopad hnízdění v pozdní fázi hnízdní sezóny na počet vylétlých mlád'at nebyl potvrzen, až na potravně bohatý rok 2017, kde k mírnému postupnému snižování počtu mlád'at na hnízdech docházelo. Mé výsledky dokumentují rozdílnou strukturu a populační dynamiku kořisti středoevropské populace sýce rousného, než s jakou se musí vypořádat skandinávská populace. Středoevropští sýci rousní tedy musí užívat odlišné potravní strategie, které jim zajistí co nejlepší reprodukční úspěšnost.

6 Introduction

Diet ecology of birds of prey has been the topic of many former studies and information gained in these studies greatly helped to determine relationships between both short-term and long-term changes in prey abundance and the success of birds of prey. The diet ecology of a large number of owl species has been studied thoroughly, especially since 1960th, usually using regurgitated pellets for determination of prey: e.g. Eagle-owl (Jaksic and Marti 1984; Papageorgiou et al. 1993; Rifai et al. 2000; Amr et al. 2016), Barn owl (Libois et al. 1983; Obuch and Benda 2009; Charter et al. 2015; Milchev 2015), Little owl (Goutner and Alivizatos 2003; Obuch and Krištín 2004; Charter et al. 2006), Tawny owl (Southern 1954; Kirk 1992; Jędrzejewski et al. 1994; Zmihorski and Romanowski 2008), Long-ear owl (Luca et al. 2001; Seçkin and Coskun 2006; Tome 2009; Hizal 2013), Ural Owl (Lowe 1980; Korpimäki and Sulkava 1987; Sidorovich et al. 2003) or Tengmalm's owl (Korpimäki 1981; Korpimäki and Hakkarainen 1991; Zárbybnická et al. 2011, 2013; Ravussin et al. 2016). However, none of these studies has focused on the interactions between prey abundance and owl diet structure using camera surveillance, even though camera analyses of owl diet can provide different (and superior) results than pellet analyses (Zárbybnická et al. 2011).

Based on the studies mentioned above, it has been shown that none of the European owl species are strict food specialists, but they usually prefer the most suitable type of prey (by size, abundance, and availability in terrain; Mikkola 1983). However, prey abundance and availability are not stable and fluctuate in space and time (Korpimäki 1984a). When there is a deficiency of the preferred types of prey, owls are constrained to hunt less favourable prey. They switch to their staple prey as soon as the level rises again, according to the alternative prey hypothesis (Hagen 1952; Lack 1954). In Scandinavia it is not an easy task, as the diversity of prey is quite low there, however, the prey diversity increases southwards (Korpimäki 1986a). Nonetheless, alternative prey is for owls more costly – either more demanding to hunt or simply less nutritious, so owls need to invest more into reproduction and their reproductive success in these food-poor years decreases (Korpimäki 1981).

The fact, that the supply of avian predators prey is usually not stable and fluctuates with either natural population cycles of small mammals (e.g. Korpimäki 1988a; Hipkiss et al. 2008; Lehikoinen et al. 2011) or agriculture management alterations

(Hakkarainen et al. 1997; Panzacchi et al. 2010; Roulin 2015) has been known and studied for quite a few decades. Raptorial birds preying on small mammals usually depend on several prey species and must deal with multiannual changes in the abundance of their preferred prey. The reproductive response of raptors to their main prey abundance may vary substantially with latitude that directly affects the regularity of small-mammal cycles (Jędrzejewski and Jędrzejewska 1996). While the higher latitude populations of birds of prey face high regular fluctuations (3-4 year cycles) of their main prey species (i.e. Microtinae voles; Hansson and Henttonen 1985; Korpimäki and Hakkarainen 1991), Central-European raptor populations are usually less limited by food supply since fluctuations in their prey population (both voles and *Apodemus* mice) are lower (Zárybnická et al. 2015a, 2017b) and main prey species are enriched with other prey species like *Apodemus* mice (e.g., Village 1990; Jędrzejewski and Jędrzejewska 1996; Salamolard et al. 2000). However, noticeable multiannual changes in the abundance of small mammals in the Central Europe region have been reported – e.g. pronounced 3-4-years period for the Common vole *Microtus arvalis* (Tkadlec and Stenseth 2001) or 3-year period for the Yellow-necked mouse *Apodemus flavicollis* (Zárybnická et al. 2013). In contrast to predominantly vole-eating Northern Europe population (with a little part of shrews and birds; Sulkava and Sulkava 1971; Korpimäki 1988a; Hörnfeldt et al. 1990), Central-European Tengmalm's owls diet regularly comprises (besides of Microtinae voles) of *Apodemus* mice, shrews, birds and occasionally dormice of the Gliridae family (Schwerdtfeger 1988; Schelper 1989; Kloubec and Vacík 1990; Pokorný et al. 2003). Both *Apodemus* mice and *Microtus* voles form in Central Europe the base of Tengmalm's owl diet and have a major impact on the breeding success of Tengmalm's owl populations (Pokorný et al. 2003; Zárybnická 2009; Zárybnická et al. 2013). Apart from the food supply, other minor factors affect prey availability, e.g. climatic conditions. In particular, increasing snow depth can reduce the availability of small mammals and delay breeding of Tengmalm's owl (Korpimäki 1986a), and even the larger owl species (being more sensitive to temperature at the beginning of breeding), like a Ural owl (Lehikoinen et al. 2011).

Inter-annual fluctuations of small mammal populations are also true for intra-annual changes of abundance. The cyclic fluctuation in the density of several boreal species of rodents can cause in some peak years a big crash in numbers, of which the driving mechanism is still a puzzle (Krebs 1994). In Fennoscandia, lemmings and voles change their population dynamics in 3 – 5-year cycles, in northern America the

period is usually 9 years and occurs notably among Snowshoe hare (*Lepus americanus*) (Hansson and Henttonen 1988). These crashes in the middle of the season may have dramatic effects on the ongoing breeding of avian predators (Korpimäki and Hakkarainen 1991). Whenever food shortage occurs during the breeding season, the earliest breeders meet the best conditions (Solheim 1983). However, in the case of a sudden descent of prey abundance, the functional response and the ability to shift to alternative prey are crucial for judging the impact of the predator on the prey species. Otherwise, the reproduction output declines. In past decades, vole population cycles can show a pattern of dampened amplitudes, sometimes explained as a possible result of climate changes (Hörnfeldt et al. 2005; Cornulier et al. 2013), but this pattern probably isn't valid globally (Korpela et al. 2014). In some cases, the long-term dampening of the prey population cycles can affect the breeding success more than lately fast-changing climate, as shown in Tawny owls (Millon et al. 2014). But even without such radical changes in prey abundance, the selection of favourite prey can shift. The proportion of main prey in Tengmalm's owl in Scandinavia (*Microtus* voles) usually changes during the season – in peak vole years, it culminates at the end of March and after that, it is relatively constant. During food-poor years the situation is different and the number of *Microtus* voles is highest in winter and afterwards gradually drops (Korpimäki 1986b). In Central Europe, there are several studies directed at within-year changes of owl diet but mostly without considering its impact on their reproduction success (e.g. Romanowski and Żmihorski 2009; Romanowski et al. 2013; Gryz and Krauze-Gryz 2016). But given that Central Europe fluctuations of small mammal populations (and therefore owls prey abundance) are overall lesser than in higher latitudes (Hansson and Henttonen 1985; Hanski et al. 1991), we can assume that the impact of these variations will also have a lesser negative effect on owl reproduction success.

Tengmalm's owl is a nocturnal avian predator with a wide Holarctic breeding range. It is greatly studied species that shows a “book example” how diet ecology varies across both space and time. In northern areas, its diet composition, breeding density and reproductive output depend on the availability of *Microtus* voles (Korpimäki and Hakkarainen 2012). On the contrary, Central-European populations exhibit no numerical responses to the availability of *Microtus* voles or *Apodemus* mice, and reproductive success relates to the abundance of *Apodemus* (Zárybnická et al. 2013). Here, in southern parts of the geographic range, Tengmalm's owl

supplements its primary prey with alternative prey such as *Sorex* shrews or *Muscardinus* dormouse (Korpimäki 1986a; Zárbynická et al. 2015e). Both fluctuations in prey abundance and snow cover create a gradient from North Scandinavia to Central Europe, to which Tengmalm's owl adapts by its foraging and migratory strategy - in Central Europe it is a generalist predator of small mammals and birds and adopts a partial migration strategy (males being resident and females nomadic), while in northern Fennoscandia (areas with pronounced vole cycles) both sexes change their strategy to nomadic Microtine specialist (Korpimäki 1986a). The sex-specific parental roles of most raptors affect their breeding radically. With females incubating and brooding, the males are providing food. Both must cooperate, and if one of them fails, the result of the nesting attempt is usually fatal (Zárbynická and Vojar 2013). More exposed to risk is the male, which can be frequently preyed upon by a diurnal bird of prey (e.g. Northern goshawk *Accipiter gentilis*) or another owl species (e.g. Tawny owl *Strix aluco* or Eagle-owl *Bubo bubo*). Although the female can be preyed upon on the nest by Pine Marten (Zárbynická unpublished data). As a result, food abundance greatly influences the reproduction strategies of Tengmalm's owls. When there is food-poor inception of the season, owls get the chance to initiate laying later when the food situation improves, according to the "food limitation hypothesis" (Lack 1946). The abundance of their primary prey predetermines owl breeding density (which is especially true for Northern Europe; Korpimäki and Hakkarainen 2012 but not for Central Europe – Zárbynická et al. 2015a), clutch size and number of fledglings (Korpimäki 1981, 1987a; Korpimäki and Hakkarainen 1991; Zárbynická et al. 2015a), occurrence of polygamy (Carlsson et al. 1987; Korpimäki et al. 2011), nestling body mass and growth rate (Zárbynická et al. 2015b), volume of laid eggs (Hakkarainen and Korpimäki 1994a) or dispersal (Korpimäki 1993).

In this thesis, I focused on studying among- and within-year changes of small mammals in relation to the structure of Tengmalm's owl diet and reproduction output. The study was performed in 2014-2017. The main hypotheses of this thesis have been settled:

- (i) Reproductive output of Tengmalm's owl would be positively related to the abundance of their main prey (*Apodemus* mice and *Microtus* voles) and it will vary among years, but it will not change rapidly within breeding seasons.
- (ii) The abundance of small mammals in the field would change over the years, and within-year changes would also occur.
- (iii) The diet structure of owls, determined based on camera monitoring using SNbox, would depend on the abundance of small mammals.
- (iv) The abundance of *Apodemus* mice and *Microtus* voles would vary during the breeding season as a result of the different timing of their reproduction.
- (v) Both *Apodemus* mice and *Microtus* voles would constitute the main prey of owls and they would substitute each other in owl diet.

7 Methods

7.1 Study site

The study was conducted in the northern part of the Czech Republic (N 50°, E 13°), on the Ore Mountain plateau (elevation: 730–960 m a.s.l.), close to the border with Saxony, during four seasons 2014-2017. The study area of approximately 140 km² in size is characterized by relics of former damage by industrial air pollution on mountain plateaus, which is lately recovering. The area is covered by Norway spruce (*Picea abies*) forest fragments, open areas and forest clearings (dominated by wood reed *Calamagrostis villosa*), solitary trees (mostly European beech *Fagus sylvatica*) and secondary growth of young trees, mainly Blue spruce *Picea pungens* (for details Zárbynická et al. 2015c), which has been cut down in recent three years because of *Gemmamyces piceae* infection. In this habitat, the Tengmalm's owl breeds primarily in artificial nest-boxes (> 90% nests; Korpimäki 1984b) as natural cavities are scarce and can be found only in rare solitary beech trees and few older spruces. From season 2014 to 2017, 212 (246 respectively) nest-boxes for the Tengmalm's owl were placed in the area of 110 km² (140 km² since 2015); they were evenly distributed within the whole study area.

7.2 Food abundance

The abundance of small mammals has been surveyed each year by the method of snap-trap captures (e.g. Korpimäki 1981, 1988; Zárbynická et al. 2013). Trapping was carried out on six quadrants (10x4 traps) four times throughout the season – in April, June, August, and October. The traps were exposed for three consequent nights and checked once a day. Each quadrant was set to represent one specific biotope – wood of *Picea abies* (2x), wood of *Picea pungens*, beechwood (2x) and open meadow area. Along these trappings, there were carried out another set of trappings on a bigger scale (3 quadrants, 121 traps each), but only twice a year (in June and October), representing summer and winter small mammal status (Att. 1). I calculated the resulting trapping index (TI) as the number of small mammals caught per 100 trap nights. Means (and SD) are shown (n = 6; n = 3 trapping localities, respectively). For the purpose of confrontal of prey trapping data versus prey recorded in nests, I interpolated the

trapping data into every day between those dates, when trappings took place. For these interpolated data I calculated the trapping index (Tab. 1).

7.3 Owl nesting data

We collected basic nesting data (clutch size, laying date and the number of fledglings) by regular inspections of nest-boxes. All nest-boxes were inspected from the onset of the breeding period (usually from late March) to the end of the breeding period (late August) within intervals from one to three weeks to detect new breeders. The nest-boxes were installed usually at the height of 3 to 5 meters above the ground. The boxes were made of raw wooden boards (20 mm thick) with dimensions of 250x250x400 mm, lined with wood chips, the distance from the top of the layer of wood chips to the box entrance was 220–240 mm, and a diameter of the opening was 80 mm.

I checked the nests weekly to measure, weigh and ring nestlings. A blood sample was taken from each nestling at least twice. These samples were used for sex determination and the analysis of blood parasites progression. The owl adults were caught, measured and ringed with a classical ring, and all female parents were also fitted with a chip ring (see below).

7.4 Owl diet

The structure of Tengmalm's owl diet was assessed using recordings made by the "Smart nest boxes" (SNbox) of our design (Zárybnická et al. 2016; Fig. 1). For camera monitoring, I chose a suitable ongoing nesting in a classical nest-box which I replaced with the camera box (n = 48). The SNboxes are standard nest-boxes augmented by further areas to allow all required components to be embedded inside. These components are electronics systems consisting of a pair of monochromatic industrial cameras with infrared lighting, IR event detector (for very fast triggering of the cameras), RFID reader (for distinguishing between male and female parent – with only female fitted with the RFID chip ring), auxiliary sensors (temperature, light sensor and

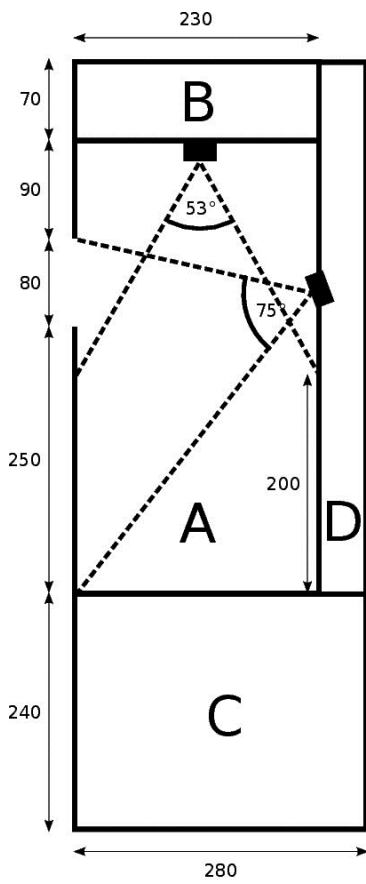
microphone), Wi-Fi router (for remote setting of user interface) and a power source (60 Ah 12 V battery) attached to one control board with dual-core processor. The adjusted box resulted in overall dimensions of 320x250x820 mm. Most of the outer box surface was covered by aluminium plate and equipped with an extended front plate and a gabled roof due to protection against nest predation by Pine marten *Martes martes*.

During 1405 days of monitoring I recorded 48 nests and in total 6392 male arrivals with prey (Tab. 4). The recordings were analysed after the end of the season and all the recorded information, like date and time of each owl activity, sex of the owl parent, type of prey, temperature inside the clutch and outside the SNbox and light intensity outside the SNbox were inserted into a data sheet. Based on the recordings I was able to distinguish 7 mammalian species: *Apodemus* mice, *Microtus* voles, *Myodes glareolus*, *Muscardinus avellanarius*, *Micromys minutus*, *Sorex araneus* and *Sorex minutus*. For the lucidity, the prey items were pooled into 4 main groups (*Apodemus* mice, *Microtus* voles, *Myodes* voles, and birds) + less common species (other). The success rate in the determination of prey is very high with this camera system (98.4% of prey items were categorized at least into genus), which showed already Zárbynická with the previous model of the camera nest box, who managed to determine 77.1 – 80.2% of delivered prey items (Zárbynická et al. 2011). Note that the diet structure of owls was only evaluated in nests that were monitored by SNboxes, not prey biomass (because of the common occurrence of prey decapitation for instance).

However, not all Tengmalm's owl nests available in 2014-2017 were monitored by SNboxes, since I was able to monitor only four simultaneously progressing nests (we had only four SNboxes available). This applies particularly for prey abundant seasons (2015, 2017). The total number of owl nests I found was 10 in 2014, 34 in 2015, 24 in 2016 and 19 in 2017. The total number of nests that I monitored by SNboxes was 48. For the nesting information on camera monitored nests during 2014-2017 see Tab. 4, for basic nesting data on all recorded nests during 2014-2017 (n = 87) see Tab. 3.

Figure 1. (a) Intelligent nest box design and its individual parts: nesting area with two cameras (marked by letter A), electronic area located in the top part of the box which stored the control

board (B), battery area located in the bottom of the box (C) and wiring area located on the back side of the box (D). Dimensions are shown in millimeters. (b) Application of the intelligent nest-box in the field.



(a)



(b)

7.5 Statistics

Multivariate data for food availability and diet composition were analyzed using Redundancy Analysis (RDA) in Canoco 5.0 software (ter Braak and Šmilauer 2012) (Tab. 2). I performed three analyses: (1) the effect of year and period on small mammal availability (by numbers), (2) the effect of year and day in season (by numbers) on diet composition and (3) the effect of year, laying date and number of fledglings on diet composition. I used a forward selection of factors. Statistical significance was obtained using the Monte-Carlo P test. Nest box ID was used as a covariate for the first two analyses. Using a linear regression analysis I examined the relationships between (1) number of nestlings present at the nest (independent variable) and a number of prey items delivered to the nest (dependent variable) with a covariate number of nest boxes); (2) number of fledglings in camera nest boxes (independent variable) and the proportion of primary prey (dependent variable) and (3) the number of fledglings in camera nest boxes (independent variable) and the proportion of individual diet groups (dependent variable). The values through the thesis are shown as mean \pm SD.

8 Results

8.1 Among-year changes in the food abundance

Significant differences in the structure of small mammal abundance between years 2014 – 2017 were found. The total number of caught individuals was 437. The overall trapping index varied from 0.60 (in 2014) to 5.79 (in 2017). The least variation in abundance showed *Sorex* shrews, with TI ranging from 0 to 0.56, the biggest was recorded in *Apodemus* mice (namely Yellow-necked mouse *Apodemus flavicollis*), with TI ranging between 0 and 5.42 (Tab. 1; Fig. 4). The most frequently trapped taxon was *Apodemus* mouse (with 52.9% of individuals), followed by Bank vole *Myodes glareolus* (with 32.3% of individuals), *Microtus* voles, in particular, *M. agrestis* (with 10.1% of individuals) and *Sorex* shrews (comprising 4.8% of individuals).

8.1.1 Year 2014

The overall small mammal abundance in the year 2014 was the lowest of recorded years (TI = 0.60), with the largest part of *Apodemus* mice (TI = 0.28). *Microtus* voles did not appear in this season at all.

8.1.2 Year 2015

Food-richer year 2015 dominated by *Apodemus* mice (TI = 2.50), *Myodes* voles were also rather abundant (TI = 1.67). The total trapping index was 4.63 on average.

8.1.3 Year 2016

Small mammal abundance in the year 2016 was low again, with TI of *Apodemus* mice dropping to 0.46. The largest portion of trapped animals took *Microtus* vole with TI = 0.56.

8.1.4 Year 2017

Season 2017 was generally in terms of small mammal abundance the most abundant (TI = 5.79) with a large representation of *Apodemus* mice (TI = 3.52) and *Myodes* vole (TI = 2.08). The quantity of *Microtus* voles returned to lower numbers (Tab. 1).

Table 1. Among-year and within-year changes in abundance (trapping index) of prey groups in April, June, and August during the study period (2014-2017), the standard deviation is in parentheses.

	<i>Microtus sp.</i>	<i>Myodes sp.</i>	<i>Apodemus sp.</i>	<i>Sorex sp.</i>	Total	No. of Individuals
2014	0 (0)	0.19 (0.21)	0.28 (0.24)	0.14 (0.24)	0.60 (0.21)	13 (2)
April	0 (0)	0.14 (0.59)	0 (0)	0.42 (0.96)	0.56 (1.07)	4 (1)
June	0 (0)	0.42 (1.29)	0.42 (1.29)	0 (0)	0.83 (1.92)	6 (2)
August	0 (0)	0 (0)	0.42 (1.29)	0 (0)	0.42 (1.29)	3 (2)
2015	0.19 (0.08)	1.67 (1.81)	2.50 (1.93)	0.28 (0.28)	4.63 (4.05)	100 (29)
April	0.14 (0.59)	0.69 (1.12)	1.25 (2.31)	0 (0)	2.08 (3.0)	15 (4)
June	0.14 (0.59)	0.56 (1.07)	1.53 (1.94)	0.28 (0.81)	2.50 (2.10)	18 (5)
August	0.28 (1.18)	3.75 (5.70)	4.72 (3.73)	0.56 (1.07)	9.31 (6.46)	67 (16)
2016	0.56 (0.84)	0.32 (0.51)	0.46 (0.42)	0.08 (0.05)	1.57 (1.54)	34 (11)
April	0.14 (0.59)	0.69 (1.44)	0.56 (1.37)	0 (0)	1.39 (1.76)	10 (2)
June	0 (0)	0.14 (0.59)	0 (0)	0 (0)	0.14 (0.59)	1 (1)
August	1.53 (3.94)	0.69 (1.88)	0.83 (1.92)	0.14 (0.59)	3.19 (4.84)	23 (4)
2017	0.14 (0.28)	2.08 (2.26)	3.52 (1.65)	0.05 (0.17)	5.79 (2.79)	125 (24)
April	0.28 (0.46)	0.69 (0.74)	0.97 (0.99)	0 (0)	1.94 (2.20)	14 (3)
June	0.14 (0.30)	3.61 (2.94)	4.17 (1.85)	0 (0)	7.92 (5.09)	57 (16)
August	0 (0)	1.94 (2.06)	5.42 (1.50)	0.14 (0.25)	7.50 (2.13)	54 (18)

8.2 Within-year changes in food abundance

No substantial within-year changes were found in the structure of small mammals within a breeding season, i.e. between trapping periods (Tab. 1; Fig. 2).

8.2.1 Year 2014

The year 2014 was characterised by low TI of all prey components since the beginning to the end of the breeding season (TI = 0.56 for all prey items together, Tab. 1). Initially, only *Sorex* shrews were available of small mammals (TI = 0.42 in April trapping). Later, a small number of Bank voles *Myodes glareolus* (TI = 0.42 in June trapping) and yellow-necked mice *Apodemus flavicollis* appeared (TI = 0.42 in June trapping). A larger increase in the population of *Apodemus* mice was not recorded until the end of the breeding season (Tab. 1).

8.2.2 Year 2015

The breeding season of 2015 began under a considerable amount of *Apodemus* mice (TI = 1.25), as well as Bank voles (TI = 0.69). The numbers were still rising to high values in *Apodemus* mice (TI = 4.72) and Bank voles (TI = 3.75) in August trapping. The other species had not reached significant values (Tab. 1). The table in Attachment 1 shows a steep increase in the abundance of Field voles *Microtus agrestis* in October (TI = 19.83), but it did not have a visible effect on Tengmalm's owl population in the next season.

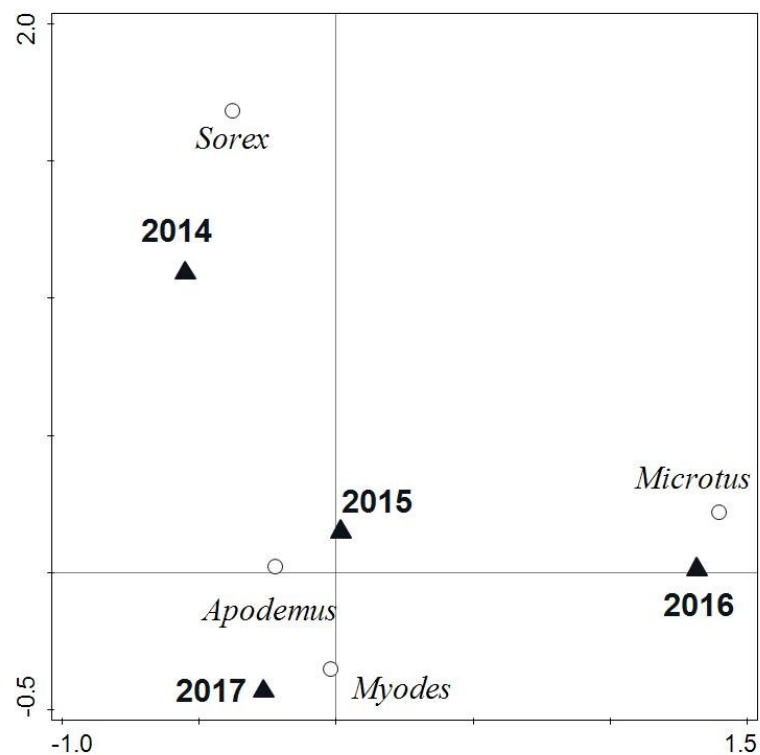
8.2.3 Year 2016

The initial numbers of main prey components at the beginning of season 2016 were average (TI = 0.56 for *Apodemus* mice; TI = 0.69 for Bank voles). But in the middle of season, the decline of all prey components occurred. There was no significant increase in the abundance of any of the prey species after that point, except for a slight increase in the Field vole population (till value of TI = 1.53 in August trapping), which, however, turned up too late to positively influence the results of the nesting season (Tab.1).

8.2.4 Year 2017

The food abundance of *Apodemus* mice (TI = 0.97) and Bank voles (TI = 0.69) was sufficient at the beginning of 2017. Both these prey groups then grew significantly (to values TI = 4.17 in *Apodemus* mice and 3.61 in Bank voles in June) and remained fairly high (TI = 5.42 in *Apodemus* mice and TI = 1.94 for *Myodes* voles) until the end of the nesting season (August). Other prey groups' abundance remained low (Tab. 1). The year 2017 was overall characterized as the most prey-abundant year.

Figure 2: Among-year and within-year differences in food abundance. RDA year, period = explanatory; locality = covariate; food availability numbers response, year3: %explain 13.8, pseudo-F = 5.0, P(adj) = 0,036. I and II canonical axes together explain 97.6% of the variability.



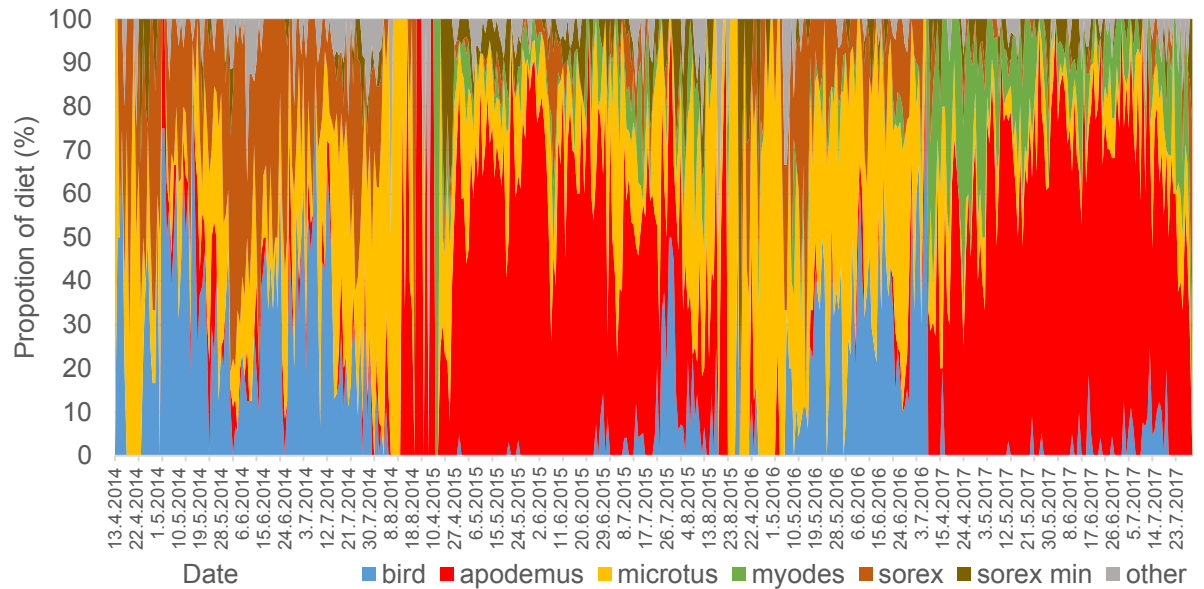
8.3 Among-year and within-year variability in owl diet composition

Based on 6392 video recordings of prey delivery by males from our SNboxes (Zárybnická et al. 2016) I was able to determine 98.4% of prey species delivered to the nests. Only a small minority of prey items (7.3%) were delivered by females, but I haven't used these data for the analysis. The structure of Tengmalm's owl prey delivered by males to their nests differed significantly between the years 2014, 2015, 2016 and 2017 (see Fig. 3; Fig. 4). The most numerous prey in owl diet – *Apodemus* mice corresponded significantly with abundance in the field ($\beta = 0.65$; $P = 0.02$), in the other prey taxa, no significant relationship was found (compare Fig. 7a, 7b). The most obvious changes among-year was recorded in the amount of delivered *Apodemus* mice (Fig. 3; Fig. 5), ranging from 3% in season 2016 to 67% in 2017. The diet varied during breeding seasons as well, in particular, *Microtus* prey increased with the day of the season (from April to August; Fig. 4) and on the contrary *Myodes* voles decreased as the breeding season proceeded (in particular, within the breeding season 2017; Fig. 4). Considering the whole period 2014-2017, Tengmalm's owl's diet dominated *Apodemus* mice comprising 42.0% of prey, followed by *Microtus* voles with 22.5% and *Sorex* shrews with 14.0% of the diet. Avian prey also formed a significant part of 11.2% and *Myodes* voles comprised 7.6% of the diet. Other rare species formed 2.7% of the diet. About 26.7% of delivered prey was decapitated or incomplete in another way).

Table 2: Results of RDA analyses for food availability and diet composition of Tengmalm's owl.

Response variables	N	Explanatory variable	Pseudo-F	P
Food availability	150	Year	4.2	0.016
Proportion of diet items	1283	Year	4.1	0.002
		Day	9.7	0.002
Proportion of diet items	48	No. fledglings	27.3	0.002
		Year	8.3	0.002
		Laying date	4.4	0.002

Figure 3: Among-year structure of small-mammal genera in the diet of Tengmalm's owl in the Ore Mountains, the Czech Republic from 2014 to 2017). No. nest = 48; No. prey items = 6392.



8.3.1 Variability in diet composition in 2014

The largest proportion of diet at the beginning of the season was comprised of alternative prey such as Common shrew *Sorex araneus* and Pygmy shrew *Sorex minutus* (both pooled form 42.9% of the diet by numbers), Field vole *M. agrestis* (33.3%) and also birds (20.6%). During the season, the proportion of *Apodemus* mice in the diet slowly grew, reaching only 7.9% in June (Fig. 4) and allowing owls to deliver a minor amount of shrews (37.9%). But the abundance of primary prey was still too small. At the end of the season, Field vole was the prevailing type of prey with 40.3% of the diet. From the recorded values, the disproportion in the relationship between food abundance in the field and owl diet and also indicate their preference for *Apodemus* mice, then for Field and Bank voles and only then for other prey (Fig. 6).

8.3.2 Variability in diet composition in 2015

The following year was fundamentally different. A higher abundance of *Apodemus* mice right from the start of the season (TI = 1.25 in April) has reflected in higher consumption of *Apodemus* mice (50.8% in the first period, 64.6% in the second period; Fig. 4). Alternative prey was practically disregarded throughout the season; only voles (represented for the most part by Field vole) formed 18.5 – 24.3% of diet during the season. At the end of the nesting season, the *Apodemus* mice were the most common prey with 47.6%, while the *Microtus* voles were the second, representing 22.9% of the diet.

8.3.3 Variability in diet composition in 2016

The 2016 season was quite a typical season with low food abundance. The numbers of *Apodemus* mice were still relatively low throughout the season (TI = 0 – 0.83) and nutrient supply was provided mainly by Field vole, whose proportion comprised 61.6% in April. However, when even those become scarce (especially in June, when their trapping index was null), they started to be replaced by birds. Bird prey constituted 20.9% in June and 46.3% in the third period (Fig. 4). Other types of prey remained relatively low – the most consumed one of them, Field vole, made up 30.6% of their diet in August.

8.3.4 Variability in diet composition in 2017

Although the abundance of *Apodemus* mice was not so low at the beginning of the breeding season (TI = 0.97), Bank voles comprising 75.0%, prevailed in owl diet in April, while *Apodemus* mice formed the remaining 25%. However, in May/June the situation changed fundamentally when larger quantities of *Apodemus* mice arrived from valleys to higher altitudes and the owls focused their attention on them (Fig. 4). Regardless of the substantial rise of the abundance of Bank voles during this period, their proportion in diet dropped to 17.1% in June. This confirms the Tengmalm's owl preference for the Yellow-necked mouse. The proportion of bird prey formed only 0 – 2.3% of diet.

Figure 4: Among-year and within-year differences in Tengmalm's owl diet. The shift of prey composition with a day of nesting is marked by the arrow. Factors with significant effect are showed. RDA year, day = explanatory; box, total = covariate; owl diet by numbers (prey groups) = response, year2: %explain 18.4, pseudo-F = 207, P(adj) = 0,002; day: %explain 1.0, pseudo-F = 11.6, P(adj) = 0,004). I and II canonical axes together explain 94.6% of the variability.

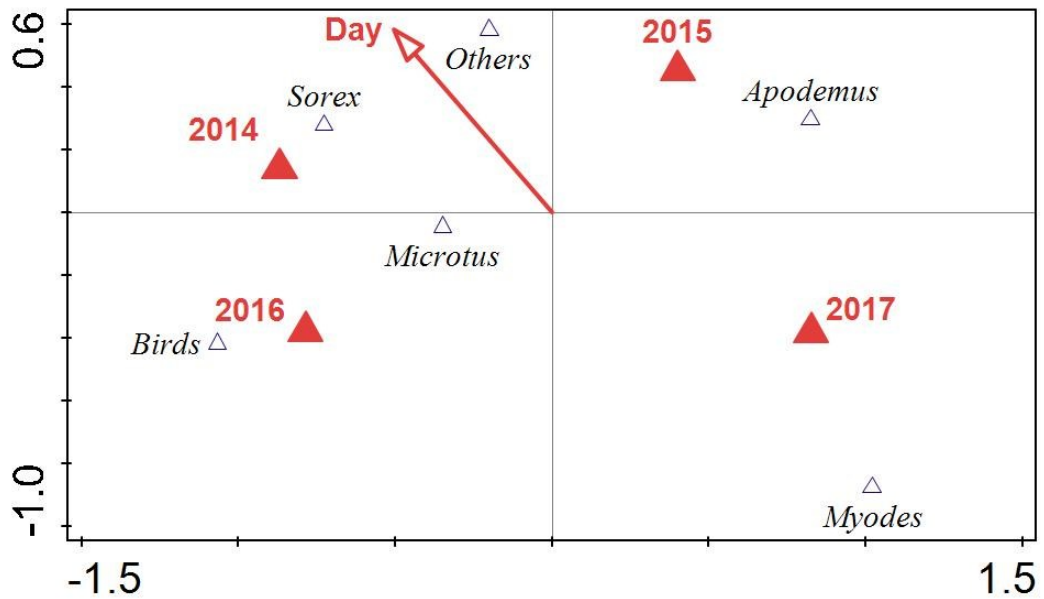


Figure 5: The development of the ratio of the most represented prey items in Tengmalm's owl diet in SNboxes during seasons 2014 – 2017 with days recalculated to three periods corresponding with the date of small mammal trappings. Number of nests: in 2014 = 8; in 2015 = 18; in 2016 = 11; in 2017 = 11. Number of prey items: in 2014 = 1306; in 2015 = 2198; in 2016 = 917; in 2017 = 1971. Note that the scales of the vertical axes differ between the panels.

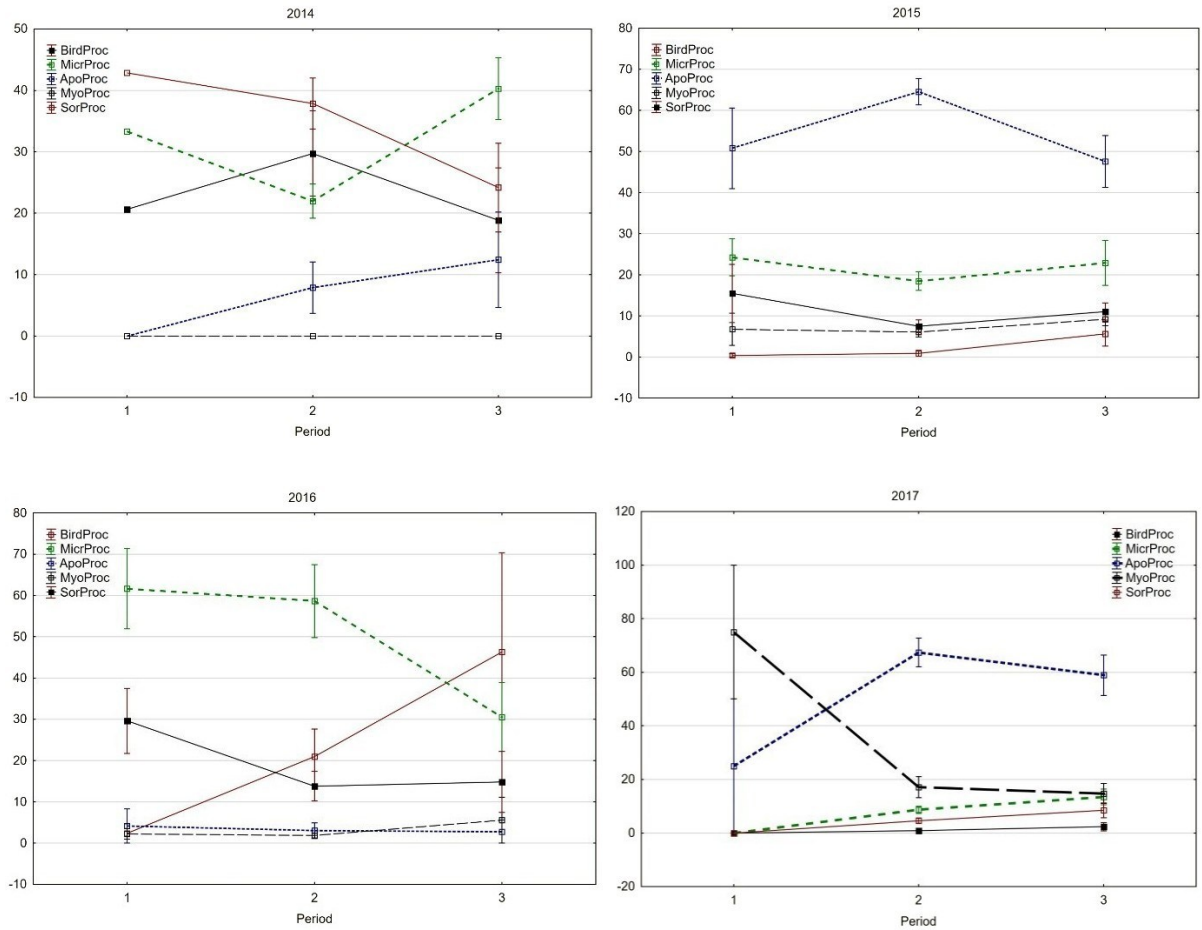


Figure 6: The proportion variation of prey groups in Tengmalm's owl diet in SNboxes within individual years 2014 – 2017. Number of nests: in 2014 = 8; in 2015 = 18; in 2016 = 11; in 2017 = 11. Number of prey items: in 2014 = 1306; in 2015 = 2198; in 2016 = 917; in 2017 = 1971.

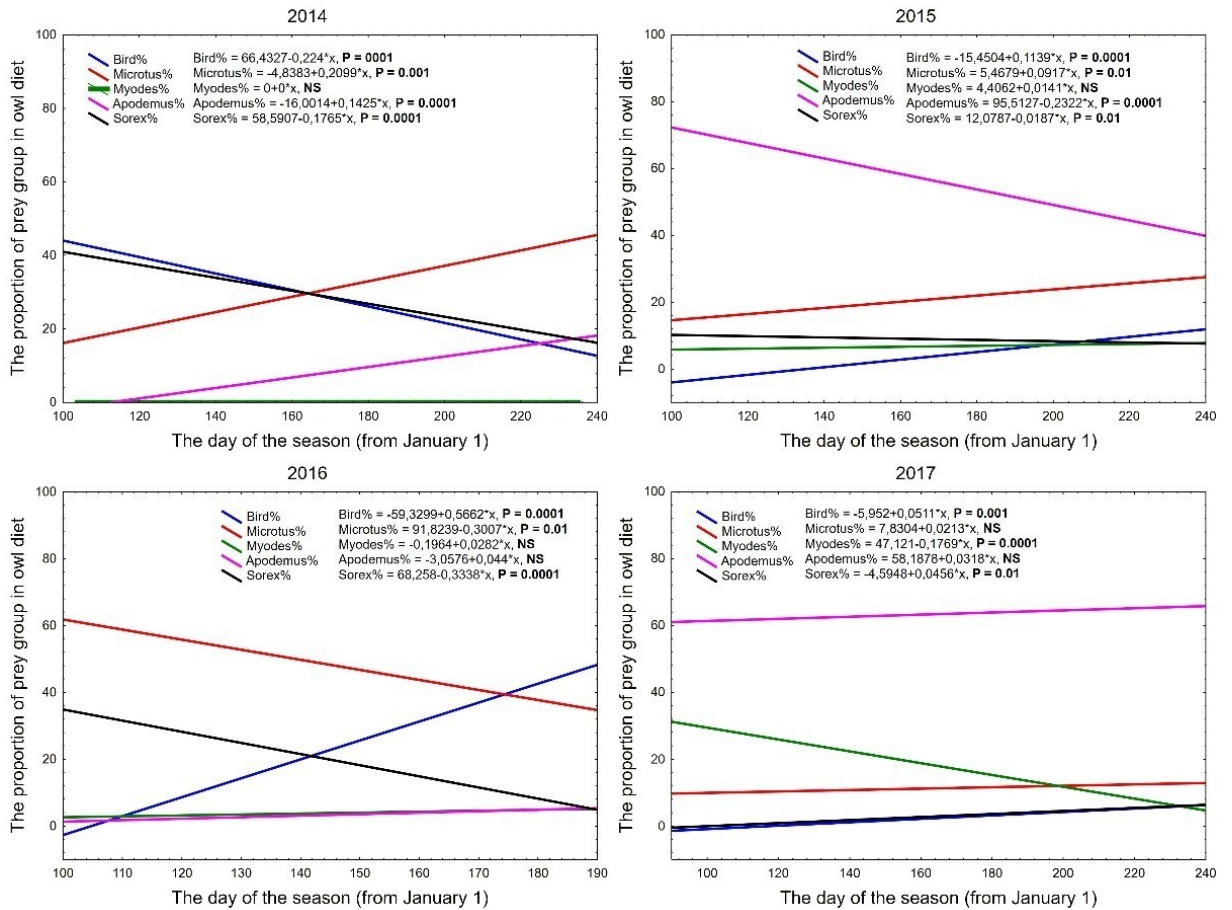
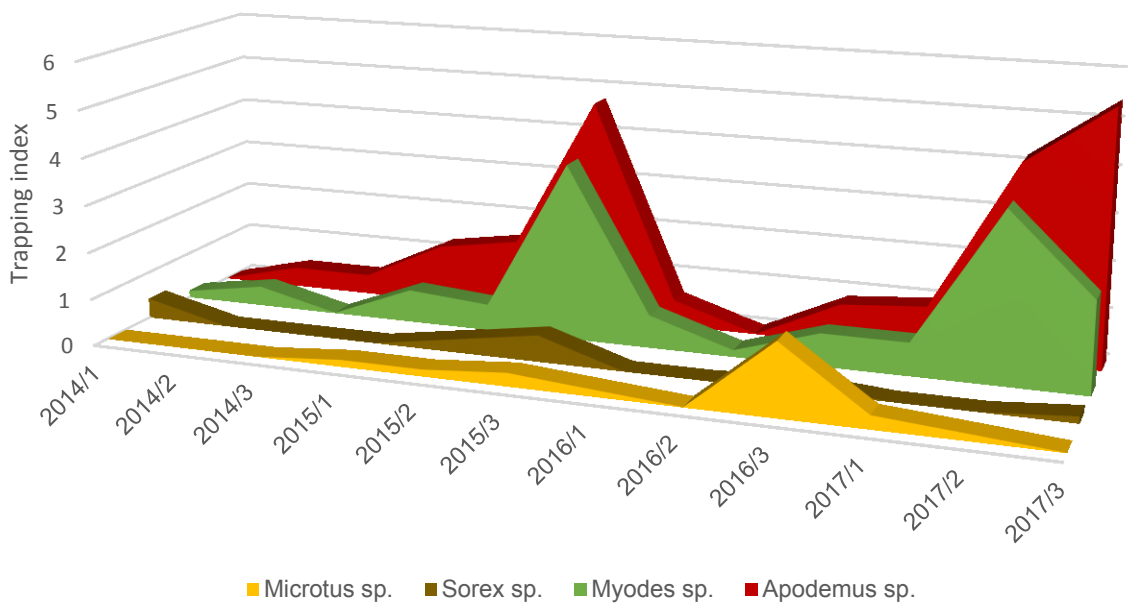
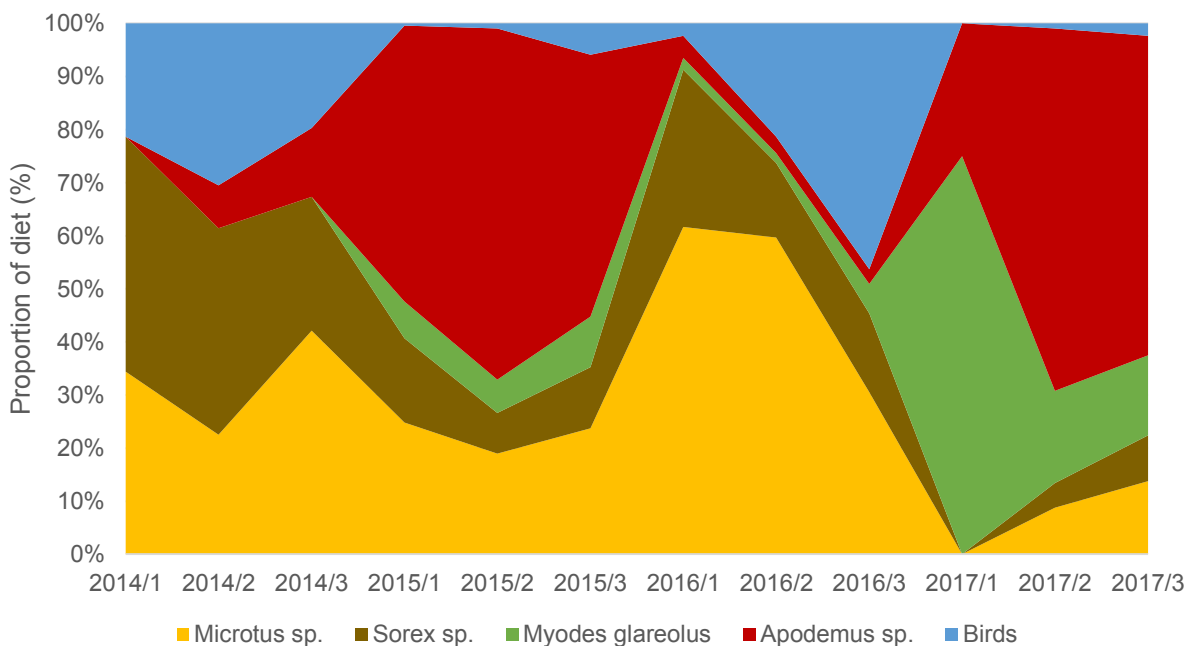


Figure 7: Changes in small mammal abundance in the field (a) and proportions of small-mammal genera in the diet of the Tengmalm’s owl in SNboxes (b) in the Ore Mountains, the Czech Republic from 2014 to 2017. Within-year diet data were converted to three periods for better comparison with trapping data. No. nest = 48; no. small mammals caught during trappings = 437; no. prey items = 6223 (169 of prey items coming under category “others” or “undetermined” were removed).

a)



b)



8.4 Feeding rate

The frequency of delivering the prey to the nest (feeding rate) fluctuated between years (Fig. 8) and depended significantly on small-mammal abundance ($\beta = 0.924$, $P = 0.08$; Fig. 7a, Tab. 1). The highest feeding rate among-years was in 2015 (5.89 ± 3.35), see Fig. 8. On the contrary, the lowest feeding rate on average was recorded in 2016 (3.56 ± 2.09), though it had an ascending tendency (Fig. 9). During season 2014 breeding owls exhibited a lower feeding rate (4.45 ± 2.89) with declining tendency, probably due to low prey abundance and smaller clutches. In 2017 the number of delivered prey was fairly high (5.63 ± 3.25). Within-year stayed the feeding rate quite stable or decreased during the season; it only rose in 2016 ($\beta = 0.852$, $P = 0.0001$) - with the lack of primary prey and voles, males were delivering prey more frequently, but mostly those of smaller-size (shrews, chicks of songbirds), see Fig. 7 and Fig. 9. The amount of food delivered directly corresponded with the number of nestlings present on a nest ($\beta = 0.661$, $P = 0.0001$; Fig. 10).

Figure 8: The number of prey items delivered by male Tengmalm's owls to their SNboxes per night in the Ore Mountains, Czech Republic. Means and SD are given. No. nests = 48; no. prey items = 6392.

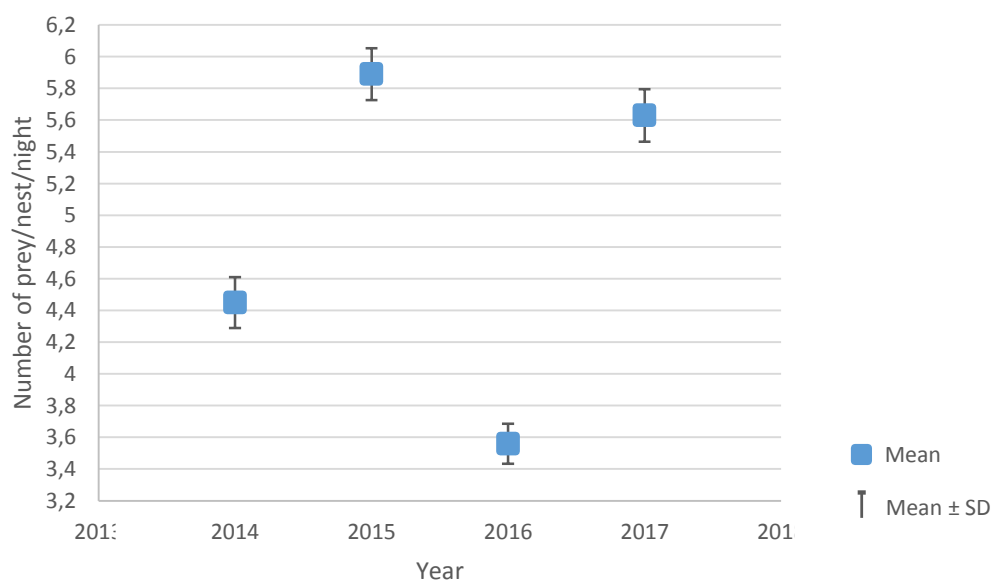


Figure 9: Feeding rate of Tengmalm’s owl males (number of male visits with prey per night) in individual SNboxes in seasons 2014-2017. Each nest has an assigned point according to the date of laying of the first egg. Number of nests: in 2014 = 8; in 2015 = 18; in 2016 = 6; in 2017 = 11. Number of monitoring nights: in 2014 = 327; in 2015 = 413; in 2016 = 276; in 2017 = 389.

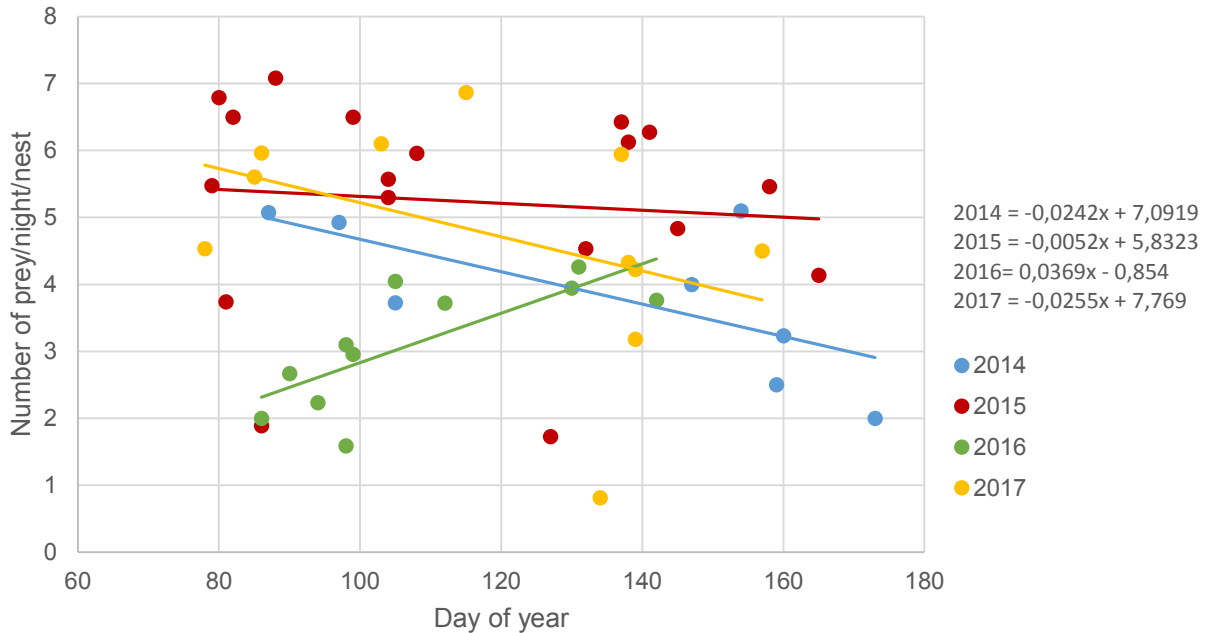
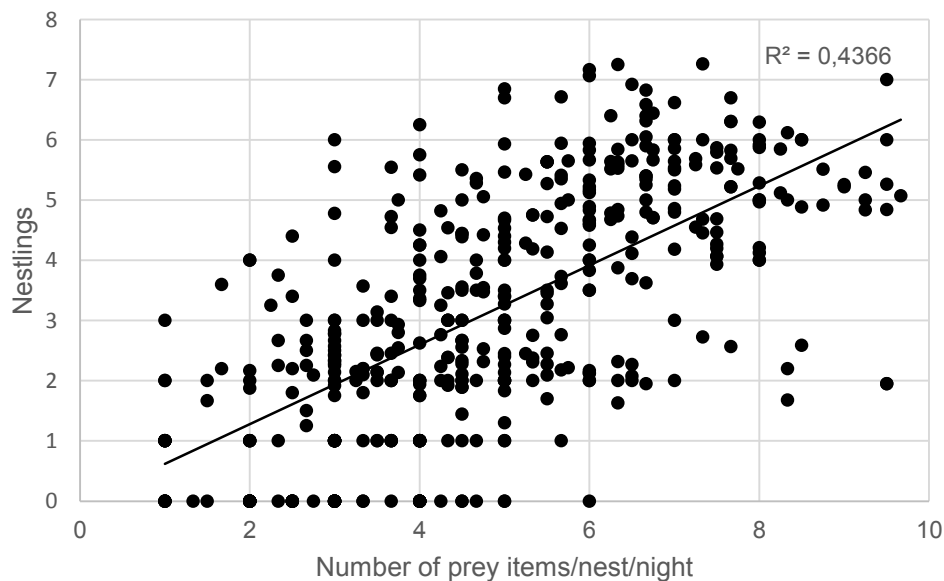


Figure 10. A relation between the number of nestlings present at the nest and the number of prey items delivered to the nest on all camera monitored nests in 2014-2017. No. nests = 48; no. prey items = 6392; no. days = 1405.



8.5 Owl reproduction – all nests

8.5.1 Reproduction in 2014

From a total of 10 nests in season 2014, eight were successful; two females abandoned the nest before completing the clutch. Mean clutch size in 2014 was the lowest recorded in my dataset (3.63/nest; SD = 0.52, n = 8). The number of fledglings stayed pretty low (1.86/nest; SD = 0.90). The season started considerably late, with the first egg laid on average on the 11th of May (SD = 33.84) (Tab. 3).

8.5.2 Reproduction in 2015

Next season, 2015, started much sooner – laying of the first egg was on average on the 21st of April (SD = 26.97) and there was the highest number of discovered nests – 34 (Tab. 3). Twenty-seven of them were successful, the remaining seven nests were deserted by parents during the incubation period. In this year, three multiple nestings of male and two sequential nestings of females were recorded. Average clutch size reached 5.41/nest (SD = 1.23, n = 27) and number of fledglings 4.19 ± 1.77 . The parental feeding rate (Fig. 8) and overall production of fledglings (113; SD = 1.62) were thus the highest of the monitored seasons (Tab. 3; Tab. 4).

8.5.3 Reproduction in 2016

First clutch sizes in season 2016 were larger than 4, but there was a dramatic drop in food abundance (Tab. 1), resulting in low overall clutch size (3.83/nest \pm 0.75; n = 6), low feeding rate and the overall nesting success – 13 nests of 24 (54%) failed entirely probably on account of a food shortage, since females deserted their clutches when the male was not able to deliver enough food to the nest (Schwerdtfeger 1984). The remaining 4 nests were preyed upon by Pine martens (*Martes martes*) (4 of 24 nests; 17%). In those nests which were not abandoned or preyed upon, there remained a low number of nestlings (2.67/nest \pm 0.52) and even fewer fledglings (1.5/nest \pm 0.55). According to the timing of breeding, season 2016 started relatively early (on average 13th of April), but due to food shortage ceased suddenly. The breeding season lasted from the 25th of March to the 11th of July, but (considering successful nestings) it was effectively much shorter (Fig. 12). Generally, the season 2016 was the shortest.

8.5.4 Reproduction in 2017

The total number of nesting Tengmalm's owls in 2017 wasn't very high ($n = 19$) and four nests were abandoned during the incubation period, one was deserted even after hatching the first nestling and one nest was preyed upon by Pine marten (*Martes martes*) during the fledgling period. But the remaining breeding pairs were exceptionally successful. Both average clutch size ($6.21/\text{nest} \pm 0.97$) and the number of fledglings ($4.79/\text{nest} \pm 2.01$) were the highest of my dataset. The duration of the breeding season was long as well, the final nesting lasted till the 24th of August, indicating steady prey abundance. Although the *Apodemus* mice were plentiful by then, the number of fledglings became somehow reduced. The average laying date was the 23rd of April. In one of the monitored nest, the male parent stopped visiting the nest relatively soon (14 days after hatching of the first nestling), so the female parent took over the food provisioning. Due to this situation, the case of cronism (eating of own nestling) occurred, when a female parent ate up five of her nestlings and only one fledgling survived.

The number of successful nestings yearly varied from 6 to 27, while the number of checked nest boxes increased during the study period only by 16 percent (from 212 to 246 nest boxes) and the study area increased proportionally. In terms of overall reproductive success (i.e. the number of fledglings per nest), season 2017 was the most successful (see Tab. 3 and Tab. 4). An essential factor for the nesting success is a sufficient food supply, especially in the period May-June (which was better in season 2017 than in 2015). The number of fledglings did not change with the day of nesting annually, with an exception of 2017, during which the number descended (Fig. 12; the camera-monitored nests only). Using RDA analyses, I found that the Tengmalm's owl breeding success (fledgling production) was affected by the structure of their diet. In particular the amount of *Apodemus* mice in diet is crucial ($\beta = 0.43$, $P = 0.003$; Fig. 11; Fig. 13; Fig. 14a). Bank voles *Myodes glareolus* in diet had a positive but only indicative effect on owl reproduction ($\beta = 0.34$, $P = 0.03$; Fig. 14b). According to nesting success, a significant negative effect was found expectedly in *Sorex* shrews ($\beta = -0.41$, $P = 0.06$; Fig. 14d) and avian prey ($\beta = -0.56$, $P = 0.0001$; Fig. 14e). Similarly negative correlation with number of nestlings had a proportion of *Microtus* voles in diet ($\beta = -0.55$, $P = 0.0002$; Fig. 14c). Other relationships were not significant ($P > 0.05$).

Table 3: Basic nesting data for all recorded nests in 2014-2017 at a research area in the Ore Mountains. No. of nests = 87. Values for clutch size, number of nestlings and fledglings are valid for successful nestings. All dates are means of all successful nests and precision is ± 2 days.

Year	No. nests (successful)	clutch size	nestlings	fledglings	laying of first egg	first hatched nestling	mean date of nesting	mean ending of nesting
2014	10 (8)	3.57	2.57	1.86	11.5.2014	13.6.2014	5.6.2014	17.7.2014
SD		0.53	1.27	0.90	30.84	33.53	35.28	31.12
2015	34 (27)	5.41	4.56	4.19	21.4.2015	17.5.2015	19.5.2015	20.6.2015
SD		1.23	1.85	1.77	26.97	27.03	30.21	31.94
2016	24 (6)	3.83	2.67	1.50	13.4.2016	19.5.2016	21.4.2016	10.6.2016
SD		0.75	0.52	0.55	27.4	27.76	34.07	42.51
2017	19 (14)	6.21	5.71	4.79	23.4.2017	25.5.2017	20.5.2017	16.6.2017
SD		0.97	1.20	2.01	27.4	27.76	34.07	42.51

8.6 Owl reproduction - camera nest boxes

Owing to SNboxes I acquired pinpoint data on laying of eggs, hatching and fledging of owlets. The results of basic nesting data (Tab. 4) generally correspond with data on all nest boxes described above (Tab. 4). The mean fledgling production is slightly higher in SNboxes due to my selection of suitable nests (explained in Discussion). Although there were 24 initiated nestings in season 2016 I was able to fully monitor only six of them, as the rest was deserted or preyed upon. For timing of breeding in individual seasons and the duration of successful nesting period, see Fig. 12. For key prey components in each year concerning fledgling production, see Fig. 11.

Table 4: Basic nesting data for all camera-monitored nests in 2014-2017 at a research area in the Ore Mountains. No. nests = 48; no. prey items = 6392; no. monitored days = 1405. Values for clutch size, number of nestlings and fledglings are valid for successful nestings. All dates are means of all successful nests and precision is ± 1 day.

Year	no. nests (successful)	mean laying date	clutch size	nestlings	fledglings	no. camera days	average no. camera days per nest	male arrivals with prey per nest
2014	8 (8)	14.5.2014	3.57	2.57	1.86	327	40.88	163.63
SD		33.38	0.53	1.27	0.90		13.56	85.25
2015	18 (18)	21.4.2015	5.50	4.94	4.63	413	22.94	119.79
SD		28.00	0.82	1.39	1.31		8.52	58.79
2016	11 (6)	21.5.2016	3.83	2.67	1.50	276	25.10	83.55
SD		13.82	0.75	0.52	0.55		14.62	60.80
2017	11 (11)	27.4.2017	6.36	6.00	5.09	389	35.36	179.00
SD		27.58	1.03	1.10	2.17		14.41	105.87

Figure 11: The fledgling production in SNBoxes in relation to prey availability and laying date. RDA fledg = explanatory; total preys = covariate; owl diet proportions = response, fled: %explain 35.2, pseudo-F = 15.7, P(adj) = 0.002). I and II canonical axes together explain 93.9% of the variability.



Figure 12: The timing of nesting (laying the first egg) and its relation with the number of successfully fledglings in all 4 seasons 2014 – 2017 in camera-monitored nests. No. nests: in 2014 = 8; in 2015 = 16; in 2016 = 11; in 2017 = 11 (the 5 remaining nests from season 2016 are not included, because they were abandoned or destroyed by predation), number of fledglings: in 2014 = 17; in 2015 = 87; in 2016 = 9; in 2017 = 56. Each nest has an assigned point according to the date of laying of the first egg.

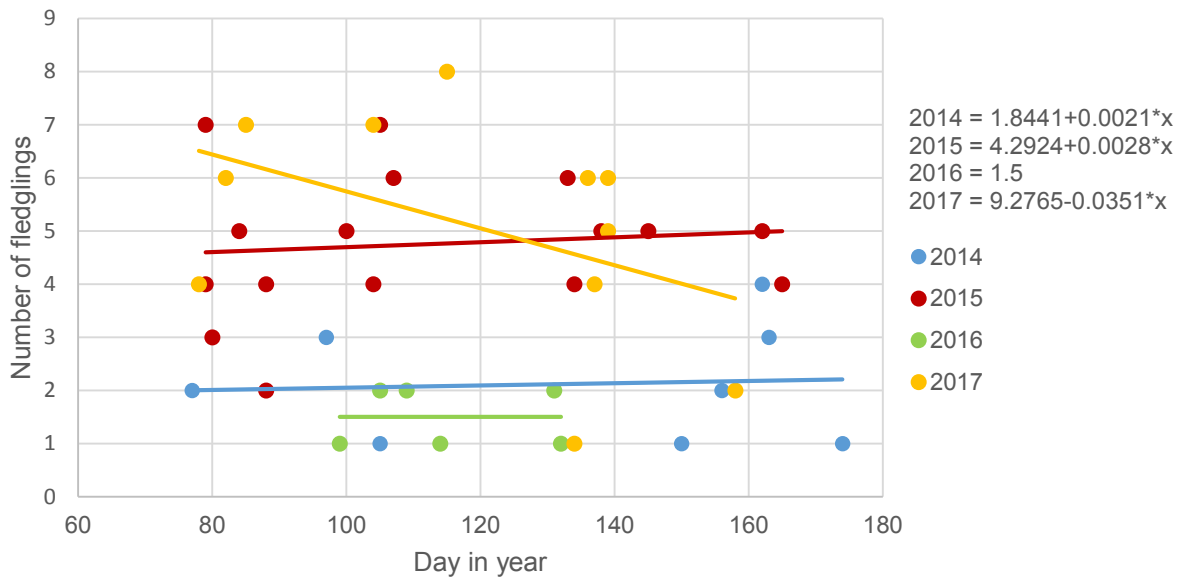
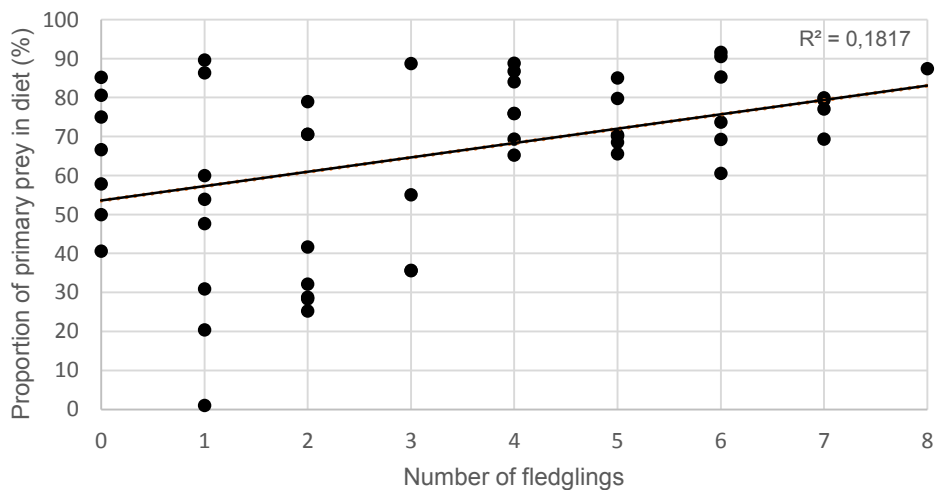


Figure 13. Reproductive output (number of fledglings) of Tengmalm’s owls in camera nest boxes in relation to the proportion of primary prey (*Apodemus* mice and *Microtus* voles combined) in the diet in 2014-2017. No. nests = 48; no. fledglings = 169.



8.7 The polyandry and polygyny

Six cases of male polygyny (7% of nestings) and three cases of female sequential polyandry (3.5% of nestings) were discovered.

The most interesting polygamous nesting was observed during the first season (2014) when, despite the lack of primary prey, one female was able to successfully raise two broods (two fledglings of the clutch of four laid eggs in first and three fledglings of the clutch of four eggs in second nesting). In both cases, the female was of substandard body mass (Šindelář et al. 2015).

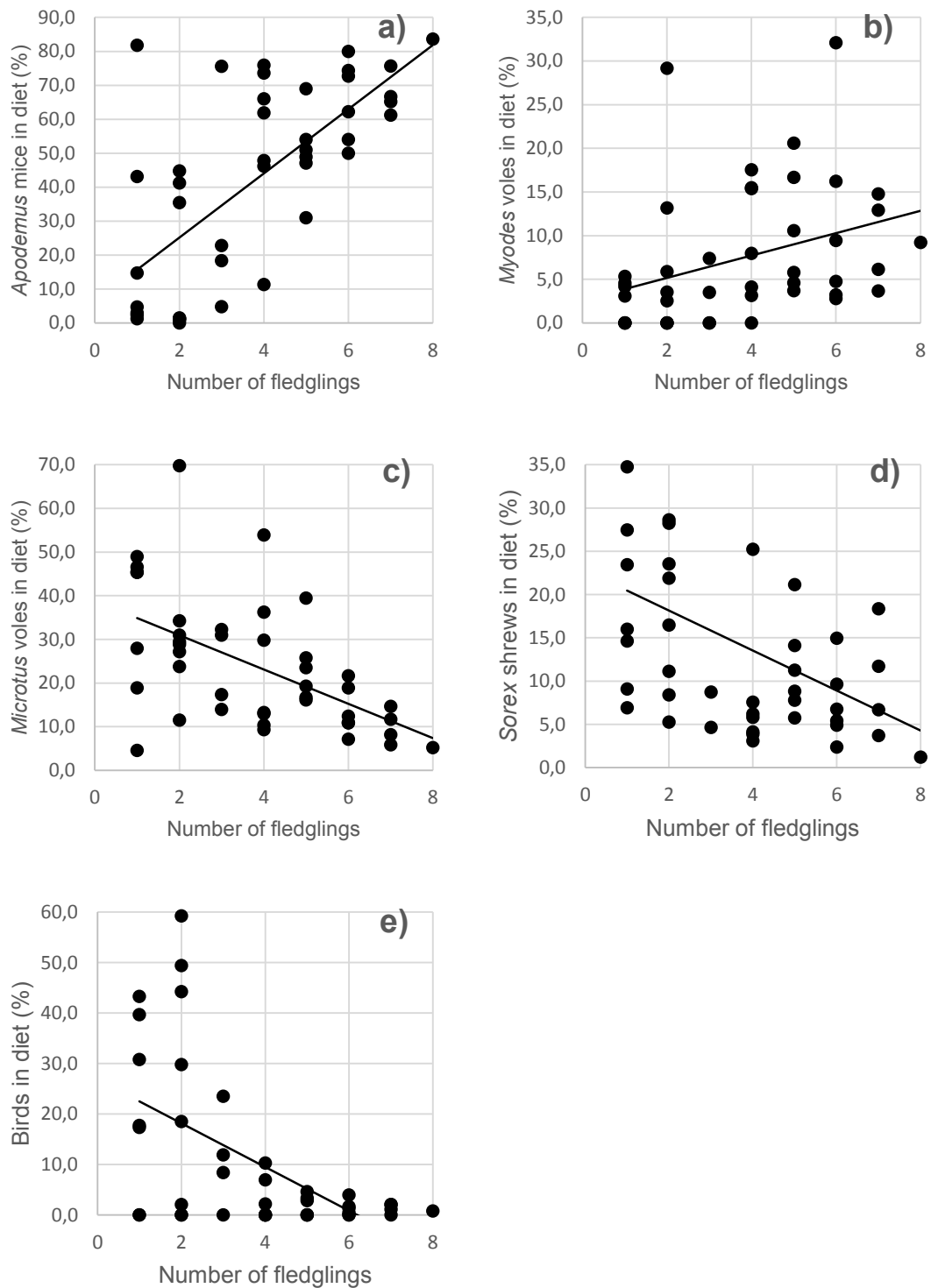
The high abundance of small mammals in season 2015 allowed more both male and female owls to utilize polygamy – four males and two females nested twice during this year. All of these males raised both their clutches successfully (at least one fledgling left the nest) with an average clutch of 4.9 (SD = 1.6) and 3.8 (SD = 1.7) fledglings (Tab. 5). Three of four of these males were polygynous and managed to supply both their nests with prey simultaneously. The fourth one nested successively. The females succeeded with only one nesting each. The first one abandoned her first nest with six eggs and raised another seven fledglings with a substitute male. The second one nurtured seven fledglings, but her second attempt to breed failed, when she abandoned her clutch of six eggs (she might have been disturbed by the installation of anti-marten protection).

During the prey-poor year of 2016, no attempt at multiple breeding was recorded. Polygyny appeared again in food rich season of 2017, when two males nested twice – both tried to feed two nests simultaneously (the timing of all four nestings was within six days) with 6.3 eggs (SD = 0.5), resulting in 2.3 fledglings (SD = 2.1). Both occupied the closest nest boxes about 200 m apart. One of them completed both nestings successfully, the second one only 50%. No female has tried to establish the second clutch this year.

Table 5: Data on polygamous individuals of Tengmalm's owl in the Ore Mountains in the Czech Republic during the years 2014 - 2017. Data are shown as a mean with \pm SD in parentheses.

season	sex	n	average clutch in polygamous nests	average clutch in all nests	no. fledglings in polygamous nests	no. fledglings in all nests	successful nestings in polygamous nests (%)
2014	M	-	-		-		-
	F	1	4 (0)	3.6 (0.5)	2.5 (0.7)	1.9 (0.9)	100
2015	M	4	4.9 (1.6)		3.8 (1.7)		100
	F	2	6.8 (0.5)	5.4 (1.2)	6.5 (0.7)	4.2 (1.8)	50
2016	M	-	0 (0)		-		-
	F	-	0 (0)	3.8 (0.8)	-	1.5 (0.6)	-
2017	M	2	6.3 (0.5)		3.0 (1.7)		75
	F	-	-	6.2 (1.0)	-	4.8 (2.0)	-

Figure 14. Projection scores of the relationship between the number of fledglings and the proportion of diet groups (linear regression): **(a)** *Apodemus* mice (df = 42, $F = 36.6$, $\beta = 0.69$, $P < 0.0001$), **(b)** *Myodes* voles (df = 42, $F = 5.5$, $\beta = 0.34$, $P = 0.02$), **(c)** *Microtus* voles (df = 42, $F = 17.5$, $\beta = -0.55$, $P = 0.0001$), **(d)** *Sorex* shrews (df = 42, $F = 8.5$, $\beta = -0.41$, $P = 0.006$) and birds (df = 42, $F = 19.1$, $\beta = -0.56$, $P = 0.0001$). Linear regressions were used. Note the scales of the vertical axe. No. nests = 43.



9 Discussion

The thesis aimed to characterize the effect of food abundance on diet composition (i.e., the functional response) and breeding success (i.e., the numerical response) of Tengmalm's owls in the Ore Mountains (Czech Republic). The research was based on a four-year camera monitoring of 48 nests (in total) with own newly developed camera nest boxes.

9.1 Prey abundance

My results have quantitatively demonstrated significant among-year and within-year dynamics of all small mammal taxon present in the area. The *Apodemus* mice showed the biggest numerical fluctuations, both inter- and intra-seasonal. In this four-year study, I found 2-year cycles in Yellow-necked mouse (*A. flavicollis*). In a 20-year time-period, Zárýbnická et al. (2017a) have documented regular 3-year cycles of *Apodemus* mice in the same study area. The population dynamics of *Apodemus* mice have been shared with Bank vole which, however, did not reach such amplitude during the study period. The overall small mammal abundance dominated with *Apodemus* mice by numbers (53% of small mammals caught). No substantial changes in habitats occurred during the study period, except for extensive logging of the Blue spruce stands in a large part of my research area at the beginning of season 2017. At that time the ground became bare of vegetation and the seedlings of new trees emerged in a large quantity. Bank vole benefits of this food source (Zárýbnická et al. 2017a) and the populations of Bank voles expanded at this time. *Microtus* voles showed relatively low levels of abundance throughout the monitored period. Since there has been documented a difference between the timing of reproduction in *Microtus* voles (the lowest numbers are in April and most abundant population occurs usually in October; Anděra and Horáček 2005) and *Apodemus* mice (the peak abundance occurs in autumn and the lowest abundance at the turn of February and March; Anděra and Horáček 2005), I anticipated this effect would reflect in the trapping results as well. Nevertheless, no significant difference has been found in the studied period – the population of both species gradually rose throughout the breeding season. I also found

that *Sorex* shrews comprised a relatively small part of trapped prey species, although there was documented that the elevation at our latitude (50°N) positively corresponds with *Sorex* shrews proportion in the field and negatively with *Apodemus* mice and *Myodes* voles, as shown by a study in the Bohemian Forest in the Czech Republic (Kloubec and Obuch 2003; Zárbybnická et al. 2017b).

9.2 Diet composition vs. prey supply

The present data recorded using a precise method of advanced camera nest boxes have shown that Tengmalm's owl reacted opportunistically to the yearly changes in the abundance of food and the amount of primary prey in their diet (*Apodemus* mice, forming 42% of diet and *Microtus* voles forming 22.5% of diet) predetermined their breeding success. The structure of owl food delivered by males differed significantly between individual years. I found a positive relationship between *Apodemus* mice availability in the field and their proportion in the owl diet. On the other hand, the abundance of *Microtus* voles, *Myodes* voles, and *Sorex* shrews did not correlate with their proportion in owl diet in any way. Therefore, my third hypothesis is only partially valid. It supports the prediction of the optimal foraging theory, which claims that the diet composition depends solely on the abundance of preferred prey and is independent of the abundance of alternative prey (Schoener 1971; Pulliam 1974). But in comparison, Korpimäki showed a pronounced positive relationship in Finland between the proportion of *Microtus* voles in the diet and their availability in the field (Korpimäki 1988a). This incoherence may be explained by the difference in the circadian activity – with *Apodemus* mice showing exclusively nocturnal activity, while *Microtus* vole activity is classified as cathemeral (Halle and Stenseth 2000). The preference for wooded habitats is mutual for *Apodemus* mice while *Microtus* voles favourite open habitats (Anděra and Horáček 2005). Given the habitat transitions in the Ore Mountains and progressive forestation in the recent 30 years, the abundance of *Microtus* voles has been slowly declining, while the abundance of forest species as *Apodemus* mice has been increasing. All these habitat features and ecological demands of two different kinds of preys may result in increased preference of Tengmalm's owl for *Apodemus* mice. In contrast, Pykal and Kloubec (1994) found no disproportion

between small mammal abundance and prey structure of Tengmalm's owl in the Šumava Mountains.

The overall high dominance of *Apodemus* mice in diet of Tengmalm's owl in the Ore Mountains ($42\% \pm 57.2$) is the most high across the entire temperate region or even for Central Europe, although other authors, who used a slightly less accurate method of determining the prey species (i.e. standard pellet method), recorded similar numbers. For example, in Western Switzerland *Apodemus* mice counted 33% (Ravussin et al. 2016), in central Serbia 35%; (Rajković 2018) or in German Saxony 37% (Wagner and Jentzsch 2000), where all studies also detected a positive correlation between gradation of *Apodemus* mice and *Myodes* voles and Tengmalm's owl clutch size. On the other hand, studies from other parts of Europe report a generally lower portion of *Apodemus* mice in Tengmalm's owl diet – for example, 7.2% in Italian Alps (Debernardi et al. 2003) or 1.4% in northeastern lowlands of Poland (Tumiel and Mirski 2018). Even in other mountain ranges of the Czech Republic, there is a considerable variation in diet structure such as the collection of samples from the Bohemian Forest has shown (containing 35.4% of *Sorex* shrews and only 11.4% of *Apodemus* mice). Jizera Mountains (dominated by *Microtus agrestis* with 43.5% and the proportion of *Apodemus* mice was 19.8%), Krkonoše Mountains (where *Microtus* voles comprised 41.3% of diet and *Apodemus* mice formed 9.5%) and Ore Mountains (containing 90.6% of *Microtus* voles and only 1.1% of *Apodemus* mice) (Pokorný et al. 2003). Nevertheless, the results from the Czech mountains were strongly affected by the time period in which the data were collected. This study took place mainly during the first half of the 1990s when the northern mountain ranges were heavily affected by industrial air pollution that destroyed the local forests for decades. During this time, high density of *Microtus agrestis*, which is a typical inhabitant of grassland of pollution clearings covered by *Calamagrostis villosa* (Heroldová 1992), emerged and on the contrary populations of *Sorex* shrews declined (Tomášková et al. 2005). Over time, the natural conditions and concentrations of sulphur dioxide, lignite, fluorides, and radionuclides are coming back to normal (Vacek et al. 2013). During the year 2017, I recorded quite an untypical change in Tengmalm's owl diet, most likely regarding the logging of the Blue spruce stands, as mentioned above. Bank voles inhabiting these new-formed bare areas probably became easy prey for Tengmalm's owl and at that time comprised more than 70% of owl diet. However, later in the season, *Apodemus* mice availability crossed some level and Bank voles apparently

ceased to be attractive as prey for Tengmalm's owl (even though their abundance was still fairly high, see Fig. 7) and were replaced by *Apodemus* mice. Avian prey accounts for roughly 25% of prey numbers in winter, but their proportions usually decrease to 3-10% in the breeding season (Korpimäki and Hakkarainen 2012). I found that during food-poor seasons the mean amount of birds in the owl diet in all nests has reached up to 47 % (during season 2016).

9.3 Diet composition vs. owl reproduction

The breeding success of the Central-European population mostly depends on the abundance of *Apodemus* mice (Zárybnická et al. 2013). It is in congruence with the present study in which I found a significant positive correlation between the proportion of *Apodemus* mice in diet and fledglings production. However, contrary to the findings of Zárybnická et al. (2013) I found a significant negative correlation between the proportion of *Microtus* voles in Tengmalm's owl diet and the number of fledglings. In the present study, only *Apodemus* mice and *Myodes* voles positively affected owl reproduction success. In the former study performed in the same area of the Ore Mountains (Zárybnická et al. 2013), only the proportion of *Apodemus* mice in the diet (forming 26.1% of owl diet composition) showed a positive relationship with the mean number of fledglings. *Microtus* voles (representing 46.8% of owl diet) showed no significant correlation with fledgling production. From an overall perspective, I suggest that *Apodemus* mice form stable main prey of Tengmalm's owl in Central Europe and both *Microtus* and *Myodes* voles are also basic components of Tengmalm's owl prey, but their importance for owls more depends on their availability in the field. In comparison to Central-European studies, *Microtus* voles in Finland substitute *Apodemus* mice (that are absent as a food supply in this area) as main prey, as was described by Korpimäki in his studies in Finland. There is the proportion of the Field vole *M. agrestis* in Tengmalm's owl diet always positively correlated with fledgling production (e.g. Korpimäki 1981, 1986a, 1988). In sum, Tengmalm's owl in Central Europe is evidently less dependent on *Microtus* vole supply than that of its Scandinavian counterpart.

The real negative effect on owl breeding success is valid for an avian prey – owls take birds only as an alternative prey because hunting birds requires larger energy

expenditure (Toland 1987), and as I detected an increased proportion of avian prey in owl diet decreases reproductive success (meaning fledgling production). I found that avian prey presented only marginal importance in owl diet within food-rich years, where it comprised less than 5% of the total diet. An increase of avian prey at the beginning of the breeding season because of the protective snow layer was described by Korpimäki (1986b), but I haven't registered this phenomenon in our study area.

There is documented that females participate in food providing only if the male parent is indisposed and unable to supply himself. Within the nests with fully functioning male, prey delivering by female occurs rarely (Eldegard and Sonerud 2009; Zárbynická and Vojar 2013). I observed similar behaviour of breeding owl pairs. I recorded the feeding rate provided by males generally reflected the availability of prey in the field and ranged from 3.56 to 5.89 individuals/100 trap nights in between-year comparison. It has been documented that Central-European Tengmalm's owls, foraging primarily on *Microtus* voles and *Apodemus* mice, exhibit lower feeding rates (i.e. 7.5 ± 1.0 prey items/nestling/night) to produce a similar number of fledglings compared to Scandinavian owls (9.2 ± 1.5 prey items/nestling/night) foraging on voles and shrews (Zárbynická et al. 2009)

I conclude that the results showed that the Tengmalm's owl reacts opportunistically to the changes in the availability of prey and widens its food niche when the preferred prey becomes scarce. It seems that alternative prey cannot fully compensate for preferred prey when it becomes rare.

9.4 Owl reproduction

Great among-year variability in the number of nests in total, hatching and fledgling productivity, and timing of breeding were recorded in four successive years of monitoring. As was mentioned above, food-rich years took changed with food-poor years and overall breeding success corresponded with the food supply. I recorded only one significant within-year change in food abundance and structure in 2016 that resulted in low breeding success of owls. During this breeding season, all kinds of small-mammalian food supply collapsed (the trapping index unexpectedly diminished from 1.39 in April to 0.14 in June) and almost all of the ongoing nesting failed. During

the whole study period, the total number of fledglings varied from nine to 113 per season (for the year 2016 and 2015, respectively).

Food abundance is also considered the ultimate factor shaping the timing of breeding in birds. The peak abundance of Tengmalm's owl primary prey usually occurs between August and October (Zárybnická et al. 2017a). Within-year variations in food supply usually favor those birds which lay eggs in a way, that the most energy-demanding stage (i.e. nestling period) coincides with the peak in food availability (Lack 1950, 1968). However, in some species, i.e. in Eurasian kestrel *Falco tinnunculus* or Eurasian sparrowhawk *Accipiter nisus*, was later documented that clutches laid in average date yield fewer fledglings than those with earlier clutches (Perrins 1965; Daan et al. 1989). This trend of monotonic decline in clutch size during breeding season seems to be typical for single-brooded nidicolous species, according to the clutch size optimization theory (Klomp 1970; Daan et al. 1989).

Contrary to this hypothesis I detected that the clutch size and number of Tengmalm's fledglings in my study did not change with the day of nesting, with an exception of 2017, during which the clutch size and number of fledglings slightly decreased in the course of the breeding season. This result is in accordance with the discovery that the clutch size decrease during the breeding season is distinct mainly during increase and peak vole years (Korpimäki 1987b). But what causes this decline? Two main explanations prevail. The first presumes a time-dependant decrease in habitat quality or food availability (the date hypothesis). The second one (the quality hypothesis) describes this productivity decline as a difference between the quality of individuals, where higher-quality individuals are able to breed earlier than the lower-quality ones (usually inexperienced novice breeders producing few eggs), as described Korpimäki and Hakkarainen in Tengmalm's owl populations in Finland (1991). Daan et al. (1989) demonstrated the negative correlation of clutch size and laying date in raptorial birds using the example of the Eurasian kestrel. Early breeding seems to be adaptive, as juveniles hatched from early clutches probably survive their first winter in a better condition and the parents gain another chance to rear a second brood (Korpimäki 1987b). Nevertheless, early breeding is not beneficial if it increases the cost of breeding due to colder weather or if food conditions are improving only later in the season. In Central Europe, it is possible for Tengmalm's owl to use the strategy of postponing nesting, if we realize that the young populations of Yellow-necked mouse *A. flavicollis*, as one of the main prey of Tengmalm's owl in the Ore Mountains,

often reach elevated areas (populated by Tengmalm's owls) later in the breeding season (Zárybnická et al. 2011). They reside in higher densities mostly in the slope parts of the plateau and their movement upwards commence with spring population growth (Kloubec and Obuch 2003; Zárybnická et al. 2017b).

Zárybnická et al. (2015c) constructed an interesting comparison of northern and Central-European Tengmalm's owl population and her results show significant differences in within-year breeding progress in those two populations. Finnish one lays larger clutches on average, but suffers from eminent within-year prey fluctuations and, therefore, high nestling mortality (Valkama et al. 2002; Zárybnická et al. 2015e), so both clutch size and nestling production radically decrease with a day of the season. The Central-Europe population shows more consistent nestlings production because here in temperate areas owls apparently benefit from a relatively stable abundance of prey and more diverse choice of alternative prey during primary prey scarcity (Zárybnická et al. 2015a).

In terms of energy use during breeding, Tengmalm's owl was characterized as "income breeder" (Korpimäki and Hakkarainen 1991), where breeding females generate energy during breeding to power the whole reproduction process in contrast with „capital breeders“, which store energy during winter and they cannot breed until they reach a certain level of built-up energy (Drent and Daan 1980). However, the capital breeding approach is applicable mainly for larger bird species and Tengmalm's owls are supposedly too small for that. The „income breeder“ model predicts independent effects of food abundance on laying date and clutch size, which is supported by significantly larger clutches produced in the increase phase of the vole cycle.

Undoubtedly, the reproductive success of Tengmalm's owl depends on the habitat surrounding the nesting site. In particular, owl reproductive success and survival rate rise with an increasing proportion of a coniferous forest area (Hakkarainen et al. 2003, 2008; Laaksonen et al. 2004). Notably, this habitat provides a safe refuge for both fledglings and adult owls against mammalian and avian predators (Bye et al. 1992; Korpimäki and Hakkarainen 2012; Zárybnická et al. 2015d).

An important strategy to augment nestling production is multiple breeding in one season. Social polyandry is a type of polygamy where the female deserts her nestlings and re-nests in the same breeding season and is often associated with uniparental care and sex-role reversal (Oring 1986; Owens 2002). Choosing this reproductive strategy

results in higher nestling production, but sometimes forces the female to abandon the nestlings nest earlier, which is reflected in a reduced survival rate in the late nestling and post-fledging stages (Oring 1986; Székely et al. 1996; Eldegard and Sonerud 2009). This type of polyandry has been documented in, at least, 9 species of raptors and 7 species of owls (Korpimäki 1988b), and has been recorded occasionally in Tengmalm's owl in a year of high food availability (Carlsson et al. 1987; Korpimäki 1991). But I recorded for the first time one case of successful sequential polyandry in a year when the abundance of primary Tengmalm's owl prey was significantly substandard and her mates were delivering to both nests mainly alternative prey - birds and *Sorex* shrews (Šindelář et al. 2015). This season was typical by overall low breeding density, delayed egg-laying (± 3 weeks later than in other monitored seasons), small clutch sizes and low reproduction success. The bodyweight of the polyandrous female was also lower than average - 157 g during the incubating period and 145 g in the second half of nestling period, while the average weight of incubating female is 181 ± 12.5 g, and in the second half of nestling period reaches 168 ± 16.8 g (Korpimäki 1990). Nevertheless, in this case, 50% of four hatched nestlings left the nest during the first breeding and 75% during the second nesting. In both nesting attempts, the two-year-old female abandoned the fledglings before they left the nests. The results of this study suggest that there are probably some other factors, in addition to food availability (e.g. breeding experience) that may play a role in Tengmalm's Owl's decisions in matters of parental care.

9.5 Nest predation

A considerable role in individual fitness and even in the life-history evolution of Tengmalm's owl may play nest predation as well. Tengmalm's owls usually suffer from Martens (*Martes* sp.) attacks, the frequency of which is habitat-dependent – more often attacked are nests surrounded by deciduous forest (Zárybnická et al. 2017c). I recorded only <6% of nests preyed upon (cf. Kloubec 2003 with 32.5% nests preyed upon, or Zárybnická et al. 2015c, where 25% of nests were destroyed by predation). Only the breeding season 2016 was struck with escalated nest predation of Pine marten (*Martes martes*) - at least, 4 of 24 nests were destroyed (while another 13 nests were deserted). This result is in line with a general allegation that mammalian predators

usually show a low predation rate in both increase and peak phases of the cycle and a high rate during the decrease and low phases (Hakkarainen and Korpimäki 1994b; Zárbynická et al. 2015c). It is because Pine marten is basically a food generalist showing functional response to the population fluctuation of its main prey (i.e. small rodents; Pulliainen and Ollinmäki 2014). The frequency of Martens predation seems to be also regionally-dependent – in SE Norway Sonerud recorded attacks on 48% of nest boxes (1985), while Korpimäki reported only 5% predation on nests in western Finland (1987c). In Central Europe, due to much higher Tengmalm's owl nesting density than in Finland (Zárbynická et al. 2015e), I would have expected proportionally higher predation. Trying to prevent Martens from getting inside the nest box I installed on every occupied nest box a metal plating with a roof, but even this barrier has been several times overcome. The best prevention against mammal predators seems to be, after all, shifting all nest boxes in which nesting took place, as Pine martens are known to revisit nest-holes they have found, even in the following seasons (Sonerud 1985; Hakkarainen et al. 2001; Kloubec 2003).

9.6 The behavioral and individual aspects

Yet, environment and population-level variations are not the only ones responsible for breeding success. Another one is inter-individual trait – the age of the mates coupled with life experience. It has been proved that two or more years old mates have generally higher breeding performance (in low and increase phase of the vole cycle in particular) than yearlings, while the age of the male has greater importance in breeding performance than that of the female (Korpimäki 1988c). The life experience of older owl individuals presents itself in their ability to nest even during a food-poor year or start laying eggs earlier in the season of increased vole abundance than the pairs of yearlings (Laaksonen et al. 2002).

One behavioural experiment was performed during a food-rich season, 2015. In one of the nests orphaned three siblings (two fledglings and one nestling). In an attempt to save them we tried to move them to another nest box. One resident young with no stored prey was in the host nest box at the time when the three unrelated young were added. The following day the resident nestling had fledged and the nest box contained only the three fostered young. Eventually, one resident juvenile from the host nest box

and two of three fostered survived until independence (they were radio-tracked). Why the foster parents accepted the unrelated young isn't clear. They possibly could have just been taking advantage of food surplus in a year of high prey abundance or the adults may not have been able to accurately distinguish their nestlings and simply fed all the young in the vicinity of their nest area (Kouba et al. 2016).

Males of Tengmalm's owl are in our latitude vocally active generally from the beginning of February till June, but in North Europe, they shift the hooting period about one month back due to the limited amount of night time in the middle of summer (Korpimäki 1981). It has been proved that males increase their effort in vocalization during a year of increased prey abundance. In those seasons their calls are both more frequent and longer (Ševčík et al. 2019). The bachelor males usually call throughout the night and even in daytime later in the breeding season (Kloubec and Pačnovský 1996). The spring trapping index of the preferred prey correlates with the mean clutch size and the number of fledglings (Korpimäki 1987a), so it obviously pays off for males to invest more energy to lure a mating partner during food-rich years, try to breed and thus build up their fitness.

The choosing of nests for camera-monitoring with larger clutches and fledgling production higher than average (compare Tab. 3 and Tab. 4) was not intentional. However, several factors could have affected my choice of suitable nests for the installation of SNboxes. Since I tried to place the SNboxes right from the start of the season I recorded mainly the nests of better quality, breeding in the early stages of the season (Korpimäki 1987c) While planning to install the SNbox I also considered female owl personality. Yes, even the personality of females was quite a strong feature. Some females were very vigilant and flew out from the nest in any sing of approach and usually roosted on a nearby tree, some of the others were much calmer and almost let me catch them with my bare hands. Certainly, we should take into account the stage of breeding, which is the most eminent variable in this respect. From my experience, a female with freshly laid eggs is most easily startled and looks out from the nest box. After 1-2 weeks, she calms down a bit and focuses more on incubating. During hatching, it is usually easy to catch her. In the nestling period, the female begins to fly out the nest more often and her reaction to a potential predator is again more vigorous. Generally, older (and repeatedly caught) females give the impression of calmer ones than yearlings.

Much other behavioural information can be extracted from high-quality SNbox recordings (e.g. storing of prey in a nest box by a female owl, nestling competition, vocal communication between parents and nestlings, female owl behaviour towards clutch or nestlings in the time of prey scarcity) in the future.

Attachment 1: Abundance (trapping index) of prey groups in June and October during the study period (2014-2017) on three complementary 11x11 quadrates.

		<i>Microtus sp.</i>	<i>Myodes gl.</i>	<i>Apodemus sp.</i>	<i>Sorex sp.</i>	Total
2014	June	0.28 (0.33)	0 (0)	0.83 (1.00)	0.28 (0.33)	1.38 (1.01)
	October	0.83 (0.50)	1.10 (0.53)	1.38 (1.67)	3.86 (1.13)	7.16 (2.47)
2015	June	2.20 (0.78)	1.38 (0.73)	6.61 (1.32)	0.83 (0.50)	11.02 (2.01)
	October	19.83 (5.39)	8.54 (4.22)	5.51 (1.48)	8.26 (3.64)	42.42 (9.28)
2016	June	1.38 (0.73)	0.83 (1.00)	0 (0)	0.28 (0.33)	2.48 (1.12)
	October	2.75 (2.32)	0.55 (0.44)	0 (0)	0.55 (0.44)	3.86 (11.05)
2017	June	0.28 (0.33)	3.86 (2.19)	11.02 (5.13)	0.28 (0.33)	15.43 (6.87)
	October	0.28 (0.33)	9.09 (5.41)	7.71 (3.62)	4.13 (1.94)	21.21 (10.70)

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