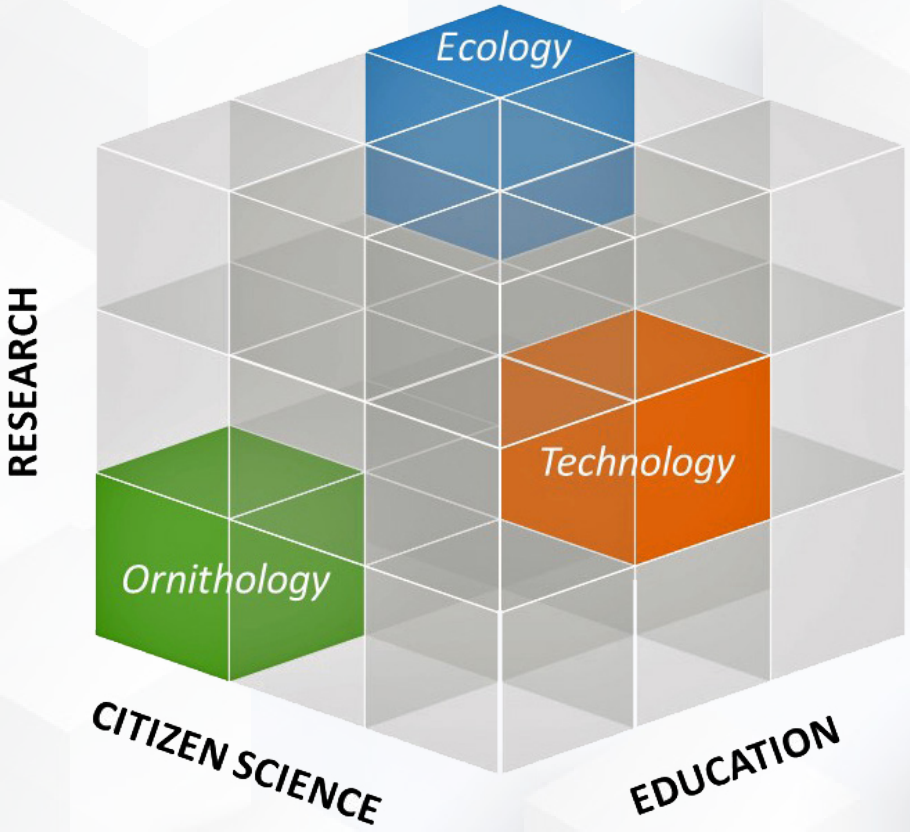
Habilitation Thesis

USING AUTOMATED DATA COLLECTION FROM NEST BOXES FOR AVIAN RESEARCH AND EDUCATION



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Contents

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1 Introduction

Birds occupy a special place in human culture and ecological research: they capture our hearts, arouse our curiosity, inspire our art, music, and religion, as well as having been economically important for human beings for thousands of years. To date, birds — approximately 10,000 living species — are the best-known of the animal classes (Lovette and Fitzpatrick 2016). One of the wonderful aspects of enjoying birds is that they are found nearly everywhere, living and reproducing in almost every environment on Earth from the most urbanized cities to the most remote wildernesses. Their ability to inhabit all habitats lies in their fascinating adaptability that has allowed the development of endlessly diverse forms of bird strategies over the last 150 million years.

The high adaptability of birds to their specific habitats makes them extremely sensitive to changes in the environment; and thus, usefully applicable as indicators of ecosystem conditions and human impacts on changes in the quality of the environment (Furness and Greenwood 1993). One such indicator is estimating population densities, which has revealed massive global losses of bird populations based on data collected by people engaged in multiple bird monitoring projects, such as the Pan-European Common Bird Monitoring project, eBird monitoring project, and many others (e.g., Both et al. 2010, Butchart et al. 2010, Rosenberg et al. 2019). Biodiversity loss has also been documented using the data collected on other animal groups, such as for instance insects (Coulthard et al. 2019, Moller 2019), but such data come from very few geographical areas and barely compete with the unique intensity with which bird monitoring is carried out. Regardless of the extent and type of data documenting biodiversity losses, we still do not necessarily know why these declines occur. To understand *why*, we need to be familiar with how birds respond to changes in their environment allowing us to identify the ecological constraints affecting the life history strategies of birds. Such understanding requires detailed information, some of which cannot be easily collected from direct human observations of birds. Instead, technological developments are required.

Advanced hardware and software are not the only means by which our knowledge of birds has been advanced. The participation of amateurs in ornithological research has a centuries-long history (e.g., Yeatman et al. 1976, Šťastný et al. 1987, Hagemeijer and Blair 1997). The relatively advanced status of our knowledge of birds can be attributed to a very substantial degree to a large group of dedicated and skilled amateur ornithologists who are often fascinated by bird behaviour and dedicate vast amounts of time to bird monitoring

(Farner and King 1973). The participation of amateur ornithologists in research has even continued to grow in importance in academic science in the last decade (Kullenberg and Kasperowski 2016). However, nowadays, in times of intensive urbanization and modern lifestyles direct interactions of people with nature are becoming more limited, and the general population’s knowledge of nature has become more restricted (Balmford et al. 2002). The need to deepen the relationships between people and their environment is the impetus for avian and environmental education. Here too, technological developments can be used, in order to facilitate formal and informal education about birds and the natural world.

In this thesis, I will be summarizing my work over the last 20 years, which comprises a combination of ecological research and public education. Much of this work could only have been accomplished because of the development of new hardware and software tools that enabled the collection and dissemination of a diverse array of data. In Chapter 2, I outline the history of using nest boxes in order to conduct research on birds, with technical advancements through time leading to the design and development of the sophisticated nest box systems that I oversaw and have used. Chapter 3 illustrates the value of such systems for collecting data in order to better understand the ecological and evolutionary forces that have shaped the nesting behaviour of my principle study species, the Boreal Owl (*Aegolius funereus*). In Chapter 4, I describe my experiences in the field of Citizen Science for the purpose of public education, work that has made use of the same tools (Chapter 2) that my collaborators and I have developed for the gathering of data for ecological research. In summary, while my main interests are in ecological research, my thesis also demonstrates how I have found connections between my ecological research and engineering and education.

List of the author's publications

Below I give a summary of my publications (listed on the Web of Science) that I included in the thesis. The main topic of each of the publications is indicated by the numbers: (1) = behavioural ecology; (2) = population ecology; (3) = landscape ecology; (4) = methodologies and developing new technologies; (5) = Citizen Science and public education. The publications that have used our purpose-designed monitoring technologies to data collection are indicated by (6). An asterisk indicates the corresponding author.

Kubizňák P., Hochachka W. M., Osoba V., Kotek T., Kuchař J., Klapetek V., Hradcová K., Růžička J., Zárybnická M.* **2019**. Designing network-connected systems for ecological research and education. *Ecosphere*. 10(6): e02761. **(4)**

Ševčík, R., Riegert, J., Šindelář, J., Zárybnická, M.* **2019**. Vocal activity of the Central European Boreal Owl population in relation to varying environmental conditions. *Ornis Fennica*. 96: 1–12 **(1)**.

Zárybnická M.*, Sklenicka P., Tryjanowski P. **2017**. A webcast of bird nesting as a state-of-the-art citizen science. *PLOS Biology*. 15(1): e2001132. (**5**)

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 Forest Research*. 63(6): 89. **(2, 3)**

Zárybnická M.*, Riegert J., Kloubec B., Obuch J. **2017**. The effect of elevation and habitat cover on nest box occupancy and diet composition of Boreal Owls *Aegolius funereus*. *Bird Study*. 64(2): 222–231. **(3,1)**

Zárybnická, M.*, Riegert, J., Šťastný, K. **2017**. Seasonal habitat-dependent change in nest box occupation by Tengmalm's owl associated with a corresponding change in nest predation. *Population Ecology*. 59(1): 65–70. **(1, 2, 3)**

Kouba M.*, Bartoš L., Tomášek V., Popelková A., Šťastný K., Zárybnická M. **2017**. Home range size of Tengmalm's owl during breeding in Central Europe is determined by prey abundance. *PLOS One* 12(5): e0177314. **(1)**

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(4): 483–492. **(4)**

Zárybnická M.*, Sedláček O., Salo P., Šťastný K., Korpimäki E. **2015**. Reproductive responses of temperate and boreal Tengmalm's Owl *Aegolius funereus* populations to spatial and temporal variation in prey availability. *Ibis*. 157(2): 369–383. **(1, 2)**

Zárybnická M.*, Riegert J., Šťastný K. **2015**. Non-native spruce plantations represent a suitable habitat for Tengmalm's Owl (*Aegolius funereus*) in the Czech Republic, Central Europe. *Journal of Ornithology*. 156(2): 457–468. **(3, 1)**

Zárybnická M.*, Riegert J, Kouba M. **2015**. Indirect food web interactions affect predation of Tengmalm's Owls *Aegolius funereus* nests by Pine Martens *Martes martes* according to the alternative prey hypothesis. *Ibis*. 157(3): 459–467. **(1, 2)**

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. **(1)**

Zárybnická, M.*, Kloubec, B., Obuch, J., Riegert, J. **2015**. Fledgling productivity in relation to diet composition of Tengmalm's owl *Aegolius funereus* in Central Europe. *Ardeola*. 62(1): 163–171. **(1)**

Kouba M.*, Bartoš L., Korpimäki E, Zárybnická M. **2015**. Factors affecting the duration of nestling period and fledging order in Tengmalm's owl (*Aegolius funereus*): effect of wing length and hatching sequence. *PLOS One*. 10(3): e0121641. **(1, 6)**

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. **(1, 6)**

Kouba M.*, Bartoš L., Zárybnická M. **2014**. Perching of Tengmalm's owl (*Aegolius funereus*) nestlings at the nest box entrance: effect of time of the day, age, wing length and body weight. *PLOS One*. 9(5): e97504. **(1, 6)**

Zárybnická M.*, Riegert J., Šťastný K. **2013**. The role of *Apodemus* mice and *Microtus* voles in the diet of the Tengmalm's owl in Central Europe. *Population Ecology*. 55(2): 353–361. **(1, 2)**

Zárybnická M.*, Vojar J. **2013**. Effect of male provisioning on the parental behavior of female Boreal Owls *Aegolius funereus*. *Zoological Studies*. 52(1): 36. **(1, 6)**

Zárybnická M.*, Korpimäki E., Griesser M. **2012**. Dark or short nights: differential latitudinal constraints in nestling provisioning patterns of a nocturnally hunting bird species. *PLOS One*. 7(5): e36932. **(1, 2, 6)**

Zárybnická M.*, Riegert J., Šťastný K. **2011**. Diet composition in the Tengmalm's Owl *Aegolius funereus*: a comparision of camera surveillance and pellet analysis. *Ornis Fennica*. 88(3): 147–153. **(1,6)**

Zárybnická M.*, Sedláček O., Korpimäki E. **2009**. Do Tengmalm's Owls alter parental feeding effort under varying conditions of main prey availability? *Journal of Ornithology*. 150(1): 231–237. **(1, 2, 6)**

Zárybnická M.* **2009**. Parental investment of female Tengmalm's owls *Aegolius funereus*: correlation with varying food abundance and reproductive success. *Acta Ornithologica*. 44(1): 81–88. **(1, 6)**

Zárybnická M.* **2009**. Activity patterns of male Tengmalm's owls, *Aegolius funereus* under varying food conditions. *Folia Zoologica*. 58(1): 104–112. **(1, 6)**

2 Global Context

In this chapter, I summarize the history of the use of nest boxes, and the use of various technologies in order to study aspects of the nesting biology of cavity-dwelling bird species. This summary leads from the initial use of nest boxes in ornithological research through to the adaptation of computer systems for use in recording data, and ends with a description of the custom-designed systems that I have used for my own research.

2.1 A review of nest boxes as a research tool

Birds have adapted to inhabit and reproduce in a variety of habitats, and one of the most fascinating capabilities is their ability to construct a variety of nests located in almost every terrestrial and shallow-water habitat on Earth. Nest location and form are very important factors for successful reproduction because they help to regulate the temperature and humidity of the nest environment, and simultaneously protect eggs and nestlings from predators and parasites (Deeming 2002). Bird species locate their nests in a variety of sites within different environments, including in cavities, burrow, sand, cracks, on the ground, cliffs, branches, and myriad human constructions (Lovette and Fitzpatrick 2016). Many cavity-dwelling bird species have also shown a preference for the use of human-made cavities — "bird boxes", "nest boxes", or "birdhouses" — attached to tree trunks, fences, walls, utility poles, or posts, where birds find suitable conditions for the location of their eggs and raising of their nestlings (Lambrechts et al. 2010, 2012).

The history of nest boxes goes back to the 15th and 16th centuries in Europe and to the 18th in the United States (Corner 2019), although human-made housing for some species, such as the Purple Martin (*Progne subis*), dates back even to before the arrival of Europeans in North America (Smith 2016). The first use of nest boxes was as a trap for eggs and chicks as food (Corner 2019). Later, since the early 19th century onwards, people have been using nest boxes to enjoy bird beauty and behaviour close around them and in the hope that insectivore birds will keep the insects off their orchards and field crops (Likens 1988, Barker and Wolfson 2013). Nowadays, one of the critical roles of nest box use is to provide suitable nesting places for birds to raise their young: nest boxes often serve as a substitute for natural tree cavities missing due to both natural and human impacts (Barker and Wolfson 2013). Dozens of kinds of boxes of different materials and sizes for a wide variety of birds and other animals are deployed (Zasadil 2001, Barker and Wolfson 2013). Boxes are mostly designed for passerines, but also for woodpeckers, falcons, owls, ducks, swifts, nightjars, and hoopoes (Zasadil 2001, Lambrechts et al. 2010, 2012, Barker and Wolfson 2013). Bird boxes, however, are often also used by mammals such as squirrels, bats, marsupials, possums, as well as reptiles and insects (for details, see Zárybnická et al. 2016).

The easy of accessibility, long lifespans, and predictable locations of nest boxes also provide motivation for ornithological researchers to use them in their studies. Nest boxes allow researchers to collect valuable knowledge on the evolutionary ecology and breeding strategies of cavity-dwelling birds that would otherwise be hidden to human understanding. The majority of such studies typically focus on investigating the abundance and breeding biology of insectivore birds species — mostly passerines (for details, see reviews Lambrechts et al. 2010, Vaugoyeau et al. 2016). An important role in the history of nest box research of passerines was played by G. Wolda, who initiated the first long-term investigation of the nest box Great Tit (*Parus major*) population in 1912 in woods in the Netherlands (Likens 1988). Later, H. N. Kluijver continued and extended Wolda's research (Kluijver 1951). Subsequently, many valuable studies, including a long-term study conducted by D. Lack in Wytham Woods, near Oxford (Lack 1955a, b, 1964; see also http://wythamtits.com), have been established.

However, nest boxes are also being used to examine species that are otherwise essentially unknown to ornithologists, such as owls. Such studies are allowing us to gain vast quantities of new knowledge on the nesting biology and food ecology of species that would otherwise be difficult to monitor. An example of such a study is the long-term study on Boreal Owl (*Aegolius funereus*; also known as Tengmalm's Owl) located in central-western Finland initiated by Erkki Korpimäki in the 1960s (e.g., Korpimäki 1981, Korpimäki and Hakkarainen 2012). Other examples are the long-term study on the same species initiated by Geir A. Sonerud in the 1980s in Hedmark county, southeastern Norway (e.g., Sonerud 1985b, Sonerud et al. 2014b), the study on Barn Owls (*Tyto alba*) established by A. Roulin in the 1990s in western Switzerland (Roulin et al. 1998, Roulin 2015), or the study on Little Owls (*Athene noctua*) conducted by Martin Šálek in the last two decades in the Czech Republic (Šálek and Schröpfer 2008, Šálek and Lövy 2012). In Chapter 3, I introduce my own 20-year study of the Boreal Owl population that I and my colleagues have conducted in air-polluted areas of the Ore Mountains, Czech Republic.

From the use of nest boxes, there are thousands of published studies resulting from the regular checking of box contents and bird nests located inside the boxes. In such studies, cavity-nesting birds often serve as model species with which to answer questions related to behaviour, function and evolutionary ecology, as well as bird conservation (Lambrechts et al. 2010, 2012, Vaugoyeau et al. 2016). Examples of research topics include population densities and dynamics over time and space (Lack 1954, 1964, Korpimäki 1981), predator-prey dynamics (Korpimäki 1984b, Visser et al. 2006, Hinks et al. 2015, Zárybnická et al. 2015c), diet and breeding ecology (Lack 1954, Sonerud 1986, Korpimäki and Hakkarainen 2012, Zárybnická et al. 2013, 2015e, Vaugoyeau et al. 2016, Grzedzicka 2018), habitat selection (Sonerud 1986, Laaksonen et al. 2004, Frey et al. 2011, Zárybnická et al. 2015d, 2017c, Caizergues et al. 2018), reproductive strategies and extra-pair paternity (Koopman et al. 2005, Lehtonen et al. 2009, Cantarero et al. 2015, Horníček et al. 2017, Abbey-Lee et al. 2018, Fokkema et al. 2018a), sex allocation (Hipkiss et al. 2002a, Hipkiss and Hörnfeldt 2004, Michler et al. 2013), and phenology (Caizergues et al. 2018, Samplonius et al. 2018), as well as the effect of nest-box quality (insulation, dimensions, nest-site depth, nest age) on reproductive success and predation risk (Korpimäki 1984a, Sonerud 1985a, b, Nour et al. 1998, Moller et al. 2014, Bleu et al. 2017, Fokkema et al. 2018b).

2.2 Advantage of indirect animal observation

Features of nest boxes, such as their conventional construction with ample inner space, water resistance, and steady location, allow more than only regular hand-operated checking of nest boxes; they facilitate the indirect observation of animals, with the basic structure of these boxes used alongside relatively recent technologies.

Indirect animal observation, using cameras, sound recording devices and other forms of data loggers (e.g., radio-frequency identification devices), is an essential methodological tool that has been evolving since the 1930s (Kluijver 1933, 1950, Gibb 1955, Royama 1959), although it has been applied most frequently in the last two decades (see below). This approach enables the non-invasive acquisition of reliable information on the ecology and behaviour of animals in their natural environments, and in situations in which direct human observation would require too much time, money and field effort, or change the natural behaviour of the observed animals (Cutler and Swann 1999, Reif and Tornberg 2006, Cox et al. 2012). Some behaviour, such as feeding and brooding the hatchlings, would never be possible to observe in cavity-nesting birds without these technologies.

Camera technologies and related devices applied for monitoring of cavity-dwelling bird species allow research into specific questions on foraging and reproductive strategies of birds. Many of these studies have dealt with foraging strategies related to quantitative and qualitative food intakes; e.g., Passeriformes (Gibb 1955, Royama 1966, Nour et al. 1998, Isaksson and Andersson 2007, Titulaer et al. 2012, Mathot et al. 2017, Injaian et al. 2018), Piciformes (Wiebe and Elchuk 2003, Gow et al. 2013, Gow and Wiebe 2014, Musgrove and Wiebe 2014), and Falconiformes and Strigiformes (Dawson and Bortolotti 2000, Zárybnická et al. 2009, 2011, 2012, Steen et al. 2010, 2011a, 2011b, 2012, Zárybnická and Vojar 2013, Sonerud et al. 2014b). Other studies have dealt with begging strategies of nestlings (Fargallo et al. 2003, Injaian et al. 2018, Mutzel et al. 2019), parental care allocation and family conflicts (Dickens and Hartley 2007, Zárybnická 2009b, Zárybnická and Vojar 2013), hatching asynchrony and brood reduction (Wiebe et al. 1998, Wiehn et al. 2000), nest attendance and activity patterns (Moreno et al. 2010, Dominoni et al. 2014, Amo et al. 2017, Bambini et al. 2019), sibling competition (Neuenschwander et al. 2003, Tanner et al. 2007, Kouba et al. 2014b), and personality (Stuber et al. 2016, Raap et al. 2018). Finally, several studies have focused on non-breeding activities of birds (Moreno et al. 2010, Dominoni et al. 2014, Amo et al. 2017, Caorsi et al. 2019).

2.3 The under-appreciated potential of the use of electronics

It has been almost 90 years since the first mechanical recorders conducted on the base of an electromagnetic circuit were mounted in nest boxes for the detection of the frequency of feeding visits by Great Tit parents (Kluijver 1933, 1950, Gibb 1955, Royama 1959). Subsequently, the development of monitoring technologies has progressed rapidly, mainly in the use of cameras, sound recording devices, and other forms of data loggers adapting technology that was developed for other purposes. Currently, edge computing and networked sensors that are central to the Internet of Things (IoT, Madhvaraj and Manjaiah 2017) are becoming a ubiquitous part of human life. However, studies on the behavioural ecology of wild animals have had been limited in the application of these off-the-shelf technologies, as well as in designing systems using features found in IoT devices that can allow for more efficient collection, management, and dissemination of a diverse array of data (Kubizňák et al. 2019).

Off-the-shelf camera systems, often used for monitoring cavity-nesting birds, provide the advantage of being a cheap, fast, and simple technical solution requiring no specific modifications of devices (Cutler and Swann 1999, Reif and Tornberg 2006). These systems, usually mounted outside of a typical nest box, allow for continual video monitoring or monitoring during a subset of time on each date, and potentially with the addition of a motion detector or IR-lighting, which are widely available in commercial camera traps (Trolliet et al. 2014). Off-the-shelf systems are also convenient when there is no need for data recording, or the records are small and data management can be performed manually. Examples of uses fitting these constraints are individuals or members of the public requiring live streaming of bird nesting (e.g., the View Nesting Birds portal; see https://viewbirds.com), or researchers who collect limited biological data such as, for example, estimating animal distributions (Junek et al. 2015), nest attentiveness (Martin 2002, Martin et al. 2007), or feeding rates (Dawson and Bortolotti 2000, Martin et al. 2000, Remes and Martin 2002, Michler et al. 2010) during a limited period of the nesting cycle.

However, the utility of off-the-shelf systems is imperfect. Most notably, each off-the-shelf device serves a single purpose, which means researchers are forced to combine multiple devices in order to collect data of different types. Additionally, off-the-shelf devices are often incompatible and inflexible, can have low reliability with a short-term life span, can be too large for use in small spaces, and are often unsuitable for outdoor use. Some devices, especially camera traps, whilst durable, can also suffer from certain specific weaknesses, such as a significant trigger delay (i.e., the time between the detection of animal activity and the first stored video frame) for video recording, dead detection zones, or the inability to detect smaller animals (for details, see Kubizňák 2014, 2019, Zárybnická et al. 2016). To achieve the required operation and to fit specific research objectives, some researchers have developed purpose-designed components that adjust, extend or synchronize the functionality of the standard off-the-shelf components, using their own purpose-designed hardware and software (Bezouška et al. 2005, Prinz et al. 2016, Suraci et al. 2017).

Custom-designed camera technologies and related networking infrastructure have been developed and used only sporadically; although these systems provide hardware and software flexibility, their functionality can exceed the technological limitations of off-the-shelf devices, and they can apply the latest features found, for example, in IoT systems (for details, see Kubizňák 2014, 2019, Zárybnická et al. 2016). Custom-designed systems are more expensive to design and produce, but they provide extended functionality. For example, they can provide simultaneous live streaming and "trapping" under various lighting conditions, allow the storage of extensive video material, reduce the trigger delay, collect a variety of ancillary data, and provide remote collection, management, and dissemination a diverse array of data, including allowing the remote controlling of systems. These systems are beneficial for researchers who need to drive the system design in order to collect data that are better matched to their research objectives (e.g., data on behavioural responses of animals to a purpose-designed motion-sensitive speaker system simulating anthropogenic disturbance; Suraci et al. 2017), or for researchers who require their systems to have specific functionality (e.g., high-speed video recording for monitoring hummingbirds; Rico-Guevara and Mickley 2017).

Both off-the-shelf and custom-designed technologies vary in how they are powered and their extent of network connectivity. The systems can be either main- or battery-powered, and either power alternative can be used with online (i.e., with an Internet connection) or offline systems (for details, see Kubizňák 2014, 2019, Zárybnická et al. 2016, Kubizňák et al. 2019). Stand-alone camera monitoring typically uses battery power, operates offline, and is used for monitoring species living in the forest and non-urban habitats where mains power is unavailable (e.g., Bolton et al. 2007, Cox et al. 2012). This approach requires manual downloading of the data and regular replacement of batteries. Offline systems save the costs for connectivity and cloud services, although they prevent the sharing of data in real time and increase costs due to the need for regular field maintenance. Internet-connected camera systems, based on wired or wireless connectivity, allow for the greatest flexibility when monitoring animals, although this approach requires relatively high costs for initial development and technical support (e.g., a reliable Internet connection). In summary, the choice of the approach should involve proper consideration of, and striking a balance between, the benefits for researchers and other participants, as well as the animals being monitored (for details, see Zárybnická et al. 2016, Kubizňák et al. 2019).

2.4 An example of a purpose-designed system for automated data collection

Since 2002, our team has incrementally designed, developed and applied various versions of purpose-designed camera systems for the monitoring of bird nests (Bezouška et al. 2005, Kubizňák 2014, Zárybnická et al. 2016, Kubizňák 2019, Kubizňák et al. 2019). We have developed two custom-designed systems for monitoring the interiors of nest boxes: *stand-alone* and *Internet-connected* systems. Below, I briefly describe the technologies and construction of both approaches, with details found in Kubizňák (2014, 2019), Zárybnická et al. (2016), and Kubizňák et al. (2019).

The core of both systems is a general-purpose computer unit (Fig. 1a–c) that connects and controls all peripheral devices, including a pair of cameras with IR-lighting (to view the nest box entrance and a nesting area; Fig. 1d–f), an IR-light activity detector (to detect each of the animal activities occurring in the nest box entrance; Fig. 1g–i), ancillary sensors (to record information on the weather and the quality of environment), and an radio-frequency identification (RFID) reader for recognition of individual birds. We embedded all the technical components in a modified wooden nest box, forming what we have termed a *Smart Nest Box* (hereafter *SNBox*). We designed the *stand-alone SNBox* (Fig. 2) for monitoring Boreal Owl nesting located in forest areas. This system was battery-powered and operated offline, requiring a manual data download. We further applied the *Internet-connected SNBox* (Fig. 3) for monitoring passerine bird nesting placed in urban areas. This system was designed as an IoT device with permanent connectivity to a university server located at the Czech University of Life Sciences in Prague, and powered from the local mains circuit (Fig. 4).

2.4.1 Stand-alone Smart Nest Box

The *stand-alone SNBox* (developed in 2014 as model 1.0), was originally created for monitoring Boreal Owl nests (Fig. 5) located in forest areas, works offline with all data being stored on a MicroSD memory card, is powered by a 12 V battery, and requires regular (every 6–7 days) maintenance to replace the battery and download the data. The system is equipped with a computer unit (Fig. 1a) featuring a heterogeneous dual-core processor, operational memory, and permanent storage. Two monochromatic industrial cameras with IR-light capability (Fig. 1d) were placed on the back of the SNBox to capture images of the nest box entrance, and on the ceiling of the box to capture images of nesting area. The cameras produce JPEG image frames at a resolution of 1280 × 1024 pixels (px) at up to 10 fps (frames per second) that are encoded to the Motion JPEG video and multiplexed with the audio channel from an external microphone. Video recording is triggered by the activity detector (Fig. 1g), and the trigger delay has been reduced to 16 ms. The embedded RFID reader, with a circular antenna, placed at the SNBox entrance, allows for scanning of the RFID tag of the passing bird in the box. To measure the local weather and environmental conditions, the model is equipped with environmental sensors: two thermometers (for interior and exterior temperature measurements) and a light intensity sensor to measure the degree of darkness. For further details, see Kubizňák (2014) and Zárybnická et al. (2016).

2.4.2 Internet-connected Smart Nest Box

The *Internet-connected SNBox* (developed as model 2.0 in 2016 and extended to model 3.0 in 2018), was designed for monitoring passerine bird nests (Fig. 6) located in urban areas, works online, and allows for the automatic collection of audiovisual data on animal behaviour and textual data on the weather and the quality of the environment. The system is equipped with a computer unit featuring a heterogeneous dual-core processor, an operational memory, permanent storage, and an integrated Ethernet circuit in model 2.0 (Fig. 1b), which was then enhanced with universal extension slots, USB connectors, a 3.5 mm audio jack, and additional connectors in model 3.0 (Fig. 1c; for details, see Kubizňák et al. 2019). Two commercial colour cameras (Closed-Circuit Television Cameras) with IR-light capability, switching automatically between the day and night modes according to the scene illumination (Fig. 1e, f), allows the system to produce colour video recordings during daytime and at dusk, and greyscale recordings in the dark. The cameras produce raw YUV video at a 1280 × 720 px resolution, which is multiplexed with the audio channel from an external microphone and encoded into the MJPEG video (model 2.0, Fig. 1e) or with the audio channel from an internal microphone to an MP4 video container (model 3.0, Fig. 1f). Video recording is triggered by the activity detector (Fig. 1h, i). Software continually creates a 3-s video buffer, whose content is prepended to all video recordings triggered by animal activity, allowing the recordings to effectively start 2–3 s before an animal enters the nest box entrance. To measure the local weather and environmental conditions, the system has been equipped with two thermometers and a light intensity sensor in model 2.0, and a thermometer, barometer, hygrometer, and photometer located at the IR-light activity detector board in model 3.0, respectively. All data are remotely transferred every day from the SNBox to a university server using a VPN tunnel (Fig. 4). The established tunnel allows automated data submission, live video streaming, remote monitoring and maintenance, and data dissemination to be performed through the university server and a web interface (Fig. 4). The university server runs a webserver, presenting all recorded data and live streams free to the public, accessible at *www.ptacionline.cz* (or *www.birdsonline.cz*). Model 3.0 uses the standard gstreamer implementation of the RTSP server to publish the live stream from the cameras. The live stream is available permanently, and multiple clients can connect at the same time. Model 2.0 only provides live streams via gstplayer to host sites. For details, see Kubizňák et al. (2019).

2.4.3 Smart Nest Box construction and installation

Both the stand-alone and Internet-connected SNBoxes have all their devices embedded in them in order to protect the whole system against inclement weather conditions, dust, insect activities, and human interference. The environmental sensors are placed as required, and a small frosted window illuminates the interior with natural light (only in the Internet-connected SNBox, Fig. 3). The overall dimensions of the SNBox are 320 × 250 × 820 mm, with a nest box entrance diameter 80 mm, for monitoring Boreal Owl nesting (Fig. 2); and 355×280×185 mm, with nest box entrance diameters 45 and 35 mm, for passerine bird nesting (Fig. 3). For details, see Zárybnická et al. (2016) and Kubizňák et al. (2019).

For the purpose of Boreal Owl nest monitoring (Fig.5, Chapter 3), we apply the stand-alone SNBox on an ongoing nesting basis, i.e., we first find an ongoing owl nest in a regular nest box and then replace it with the SNBox. This requires catching an incubating (or brooding) female and replacing her original box, including the nest contents, with the SNBox. In total, we have managed four SNBoxes that we applied across four breeding seasons (April–August), between 2014–2017, with most owl pairs accepting their new "home". However, some owl individuals (14.7%, 10 of 68 nesting attempts) deserted their SNBoxes one or two days after the installation of the SNBox, the reason(s) for which we have not yet been determined. Regardless, the frequency of such desertions did not reach or exceed the rate of abandoned owl nests in nature in our study area (25.3%, 84 of 332 nests in 1999–2018).

For the purpose of monitoring passerine bird nesting (Fig. 6), we do not replace any original nest boxes with the SNBox. Instead, we install the Internet-connected SNBoxes (as part of the Birds Online project; see Chapter 4) in areas where natural nesting sites are typically in short supply and nest boxes are usually readily occupied by passerines. We usually install the SNBoxes on trees, and less commonly on loggias of blocks of flats, windows, or walls of the buildings, and electric poles (see Chapter 4.2 for details), and use PoE (Power over Ethernet) technology to provide the Internet connection and the electric power. In total, we have managed 57 SNBoxes since 2016 (for details, see Chapter 4).

2.4.4 Extraction of information

Once data have been downloaded manually via an Ethernet cable (model 1.0) or stored automatically on the server (model 2.0 and 3.0), we extract the information from the audiovideo and contextual data. As part of the automated process of data extraction, we perform the data-management process of attaching to each video recording a set of *contextual information* including: the ID of the computer unit, the date and time of each activity, the number of the RFID chip, the size of the video file, the temperature (°C) outside and inside the box, the outside light-intensity (Lux or dimensionless number), the humidity (%), and the pressure (hPa). Based on manual evaluation of the video contents (Fig. 5, 6), we identify the *biological information*, including: the bird/animal species, the bird individual, the number of eggs and nestlings, the entrances or departures to/from the SNBox by bird individuals, prey deliveries, consumption of prey and removal of droppings, the structure of prey and nest material, egg covering by the nest material, egg incubation and arrangement, feeding of nestlings and dismembering of prey, visual and acoustic communication between individuals, perching of nestlings in the nest box entrance, and departures from the box by the fledglings. Finally, we also identify the predators of nesting birds and extract data on non-breeding activities of animals during the entire year (for details, see Zárybnická et al. 2016, Kubizňák et al. 2019).

Figure 1. Electronic components and peripheral devices of the model 1.0, 2.0, and 3.0 Smart Nest Box (SNBox). The custom-designed computer unit in the open plastic housing of the model (a) 1.0, (b) 2.0, and (c) 3.0 SNBox. The industrial camera of the model (d) 1.0 SNBox and the commercial camera of the model (e) 2.0 and (f) 3.0 SNBox with IR lighting and a custom-designed housing in a box with a transparent lid. The custom-designed IR-light activity detector of the model (g) 1.0, (h) 2.0, and (i) 3.0 SNBox. Note that the model 3.0 cameras are equipped with integrated microphones, while the model 1.0 and 2.0 computer unit is fitted with a custom external microphone. For further details, see Kubizňák et al. (2019).

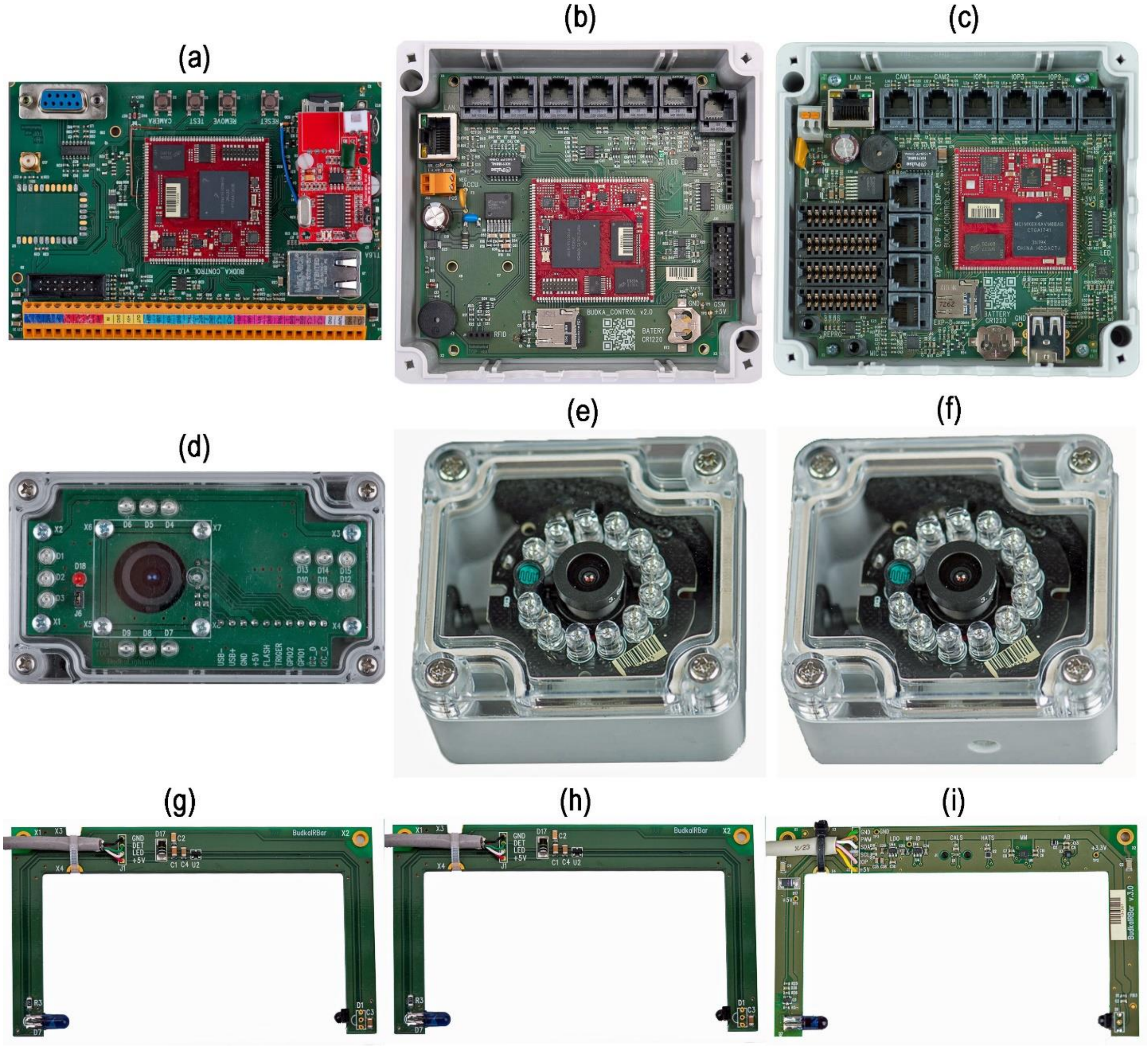


Figure 2. The stand-alone Smart Nest Box (SNBox). (a) The design of an original wooden construction of the model 1.0 SNBox for monitoring Boreal Owl nesting in forest areas. (b) Design and dimensions (in mm) of the SNBox and its individual parts: a – the nesting area (designed to place the first camera opposite the nest box entrance to capture images of the entering and leaving owl's individuals and to locate the second camera on the ceiling of the box to capture images of nesting area); b – the electronic area (used for storing the computer unit); c – the battery area; and d – the wiring area. For more details, see (Zárybnická et al. 2016).

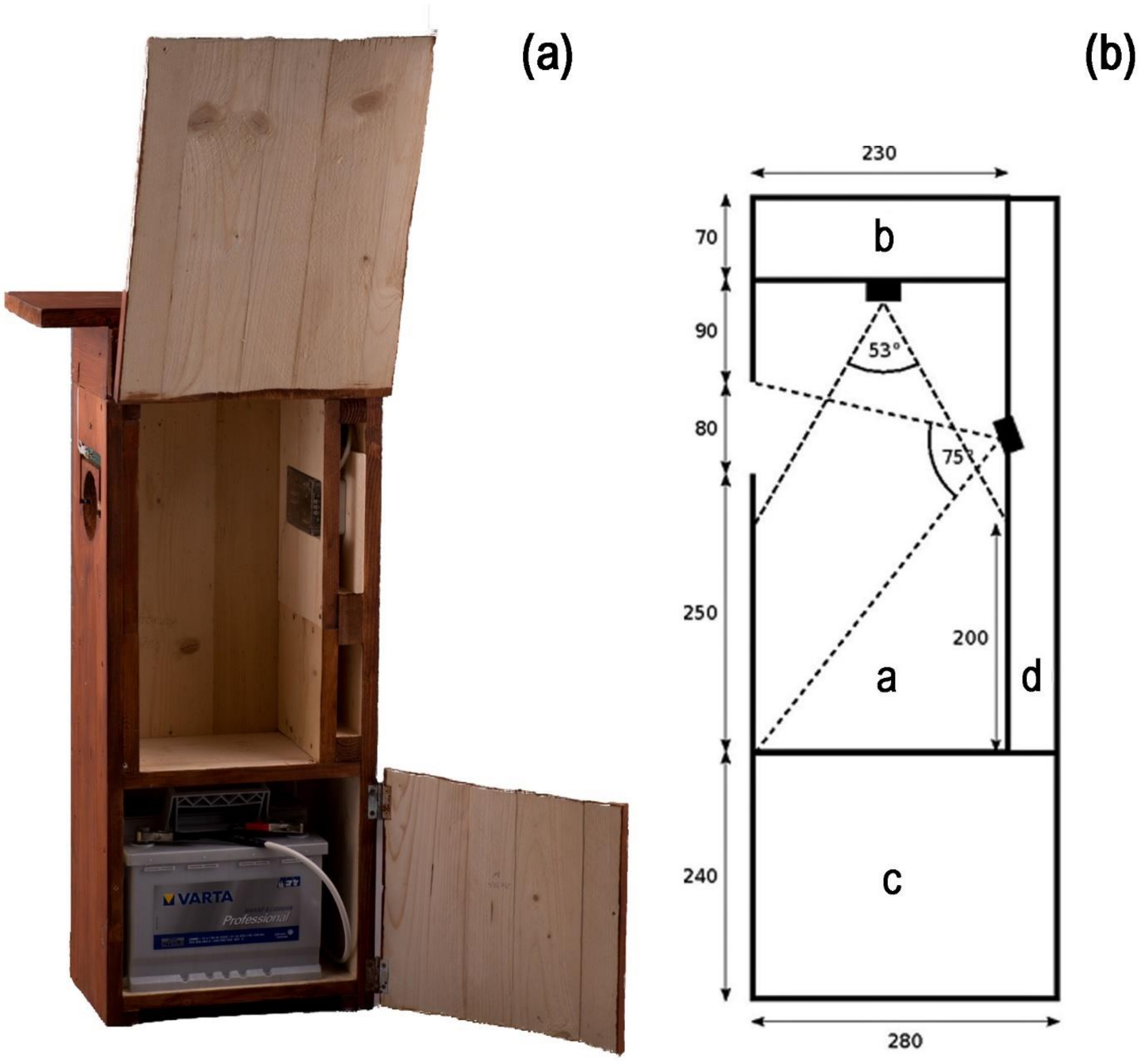


Figure 3. The Internet-connected Smart Nest Box (SNBox). The design of an original wooden construction of the model 3.0 Smart Nest Box (SNBox) for monitoring passerine bird nesting in urban areas and its individual parts. (a) The completed SNBox. (b) A front view of the SNBox exposing the IR-light activity detector board upon which environmental sensors were also located. (c) The inner SNBox space containing a nesting area with one or two cameras and the electronics area with a computer unit and cabling. (d) Side view of the SNBox with uncovered window and exterior light and temperature sensor (model 2.0 only). (e) Photo and schematic of the front wooden cover with the entrance (35 or 45 mm) and the lens used to direct light to the illumination sensor. (f) Schematic of the box and its individual parts: a – the nesting area; b – the electronic area; c – the front wooden cover; d – the window shielded by translucent plexiglass and covered by a removable cover. Outer dimensions are in millimetres. Note that the model 2.0 box only differed in the front wooden cover, which did not include the lens, and environmental sensors were located on the outside wall instead of the IR-light activity detector board (e). For more details, see Kubizňák et al. (2019).

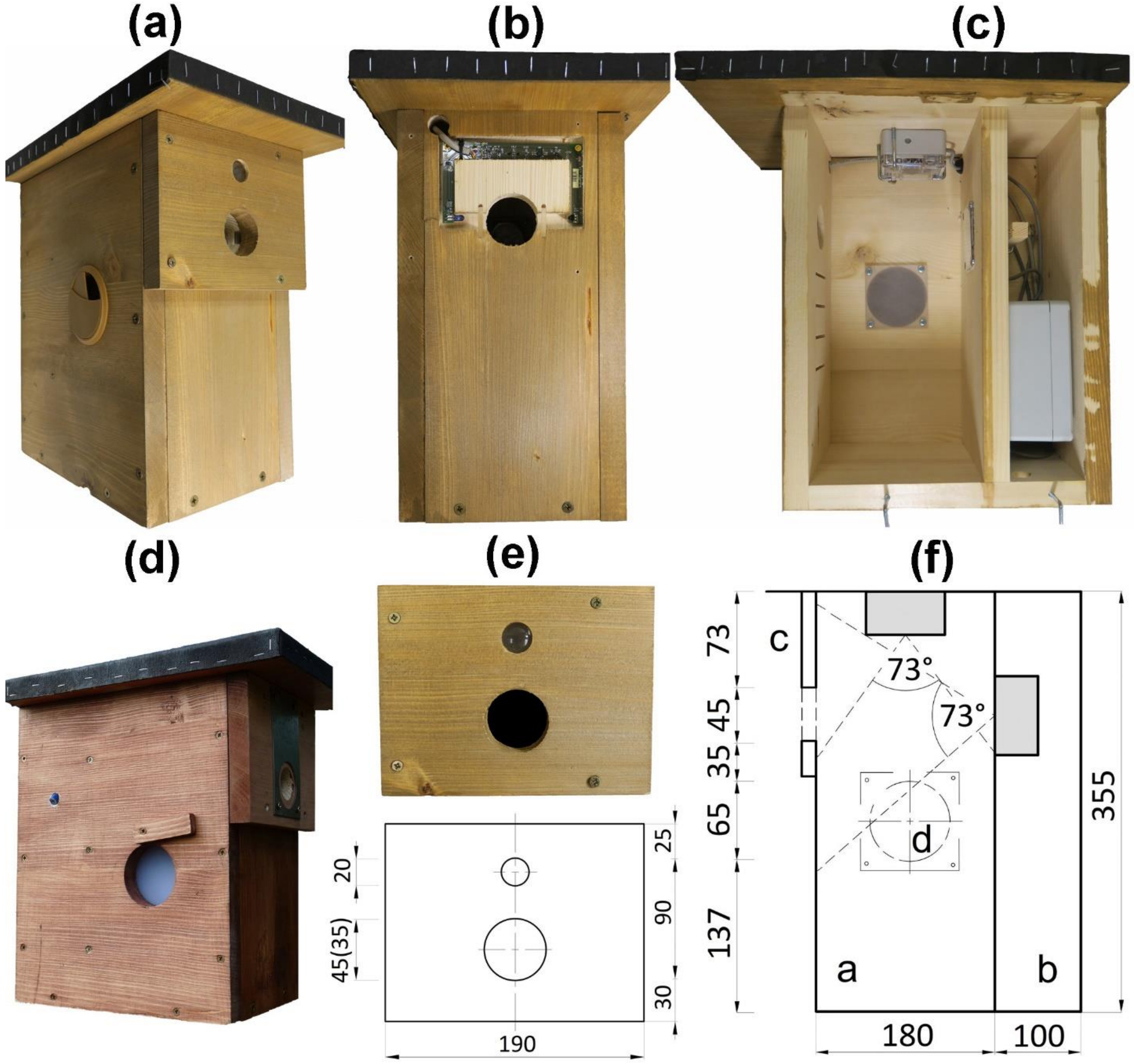


Figure 4. A schematic of the networking infrastructure of the Smart Nest Box (SNBox) camera system (model 2.0 and 3.0). (a) The SNBox installed at the host locality. (b) PoE (Power over Ethernet) adapter. (c) Host's router, a central point of the LAN (Local Area Network), and the gate to the WAN (Wide Area Network). (d) Local user PC. (e) The Internet interconnecting all devices together. (f) University server (ptacionline.czu.cz) running all server-side services. (g) Server-side data storage. (h) Webserver, accessible via www.ptacionline.cz and www.birdsonline.cz. (i) Remote user PC. For further details, see Kubizňák et al. (2019).

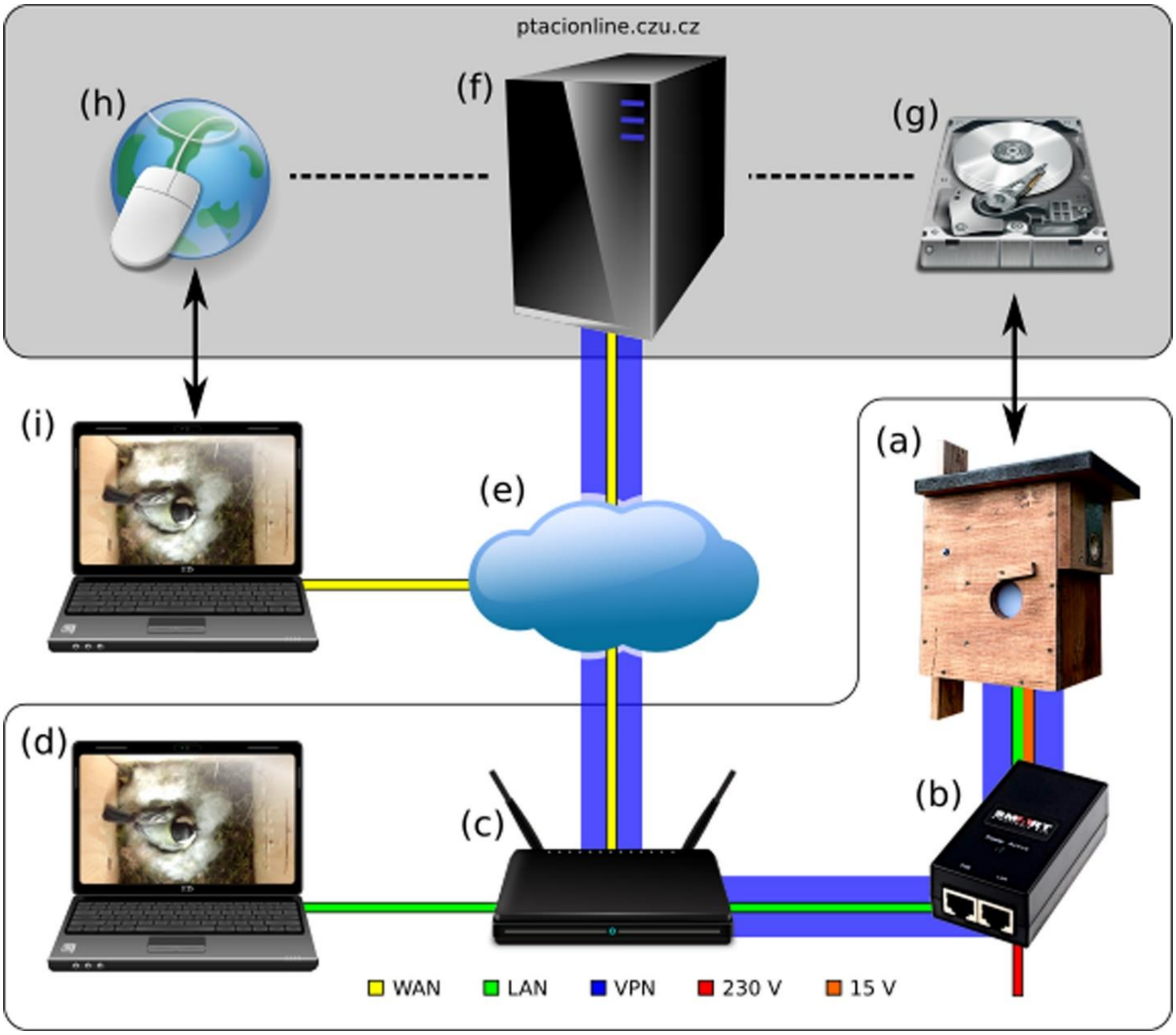


Figure 5. Examples from videos documenting Boreal Owl nesting recoded by the stand-alone Smart Nest Box (SNBox). Snapshot of (a) an incubating female; (b) nestlings in the fledgling period; (c) a female (lower positioning) and male (upper positioning; note that it is very rare for a male to enter the box and then remain there with the female, even for just a few seconds); (d) a female with her nestlings; (e) a fledgling; (f) a Pine Marten (*Martes martes*) individual predating on an owls' nest; (g–p) a male delivering (g) an *Apodemus* prey, (h) a Hazel Dormouse (*Muscardinus avellanarius*) prey, (i) a Bank Vole (*Myodes glareolus*) prey, (j) a *Microtus* prey, (k) a *Sorex* prey, (l) a decapitated *Microtus* prey, (m) a thrush nestling prey, (n) a bird nestling prey, (o) the remains of a bird prey, and (p) a bird prey (Common Chaffinch, *Fringilla coelebs*) to the female; (q) a female coming into the SNBox after a short time-out from incubating; and (r) stored prey, eggs, and a hatchling.

(a)

(b)

(c)

(d)

(e)

(f)

(g) (h)

(i) (j)

(k) (l)

(m)

(n)

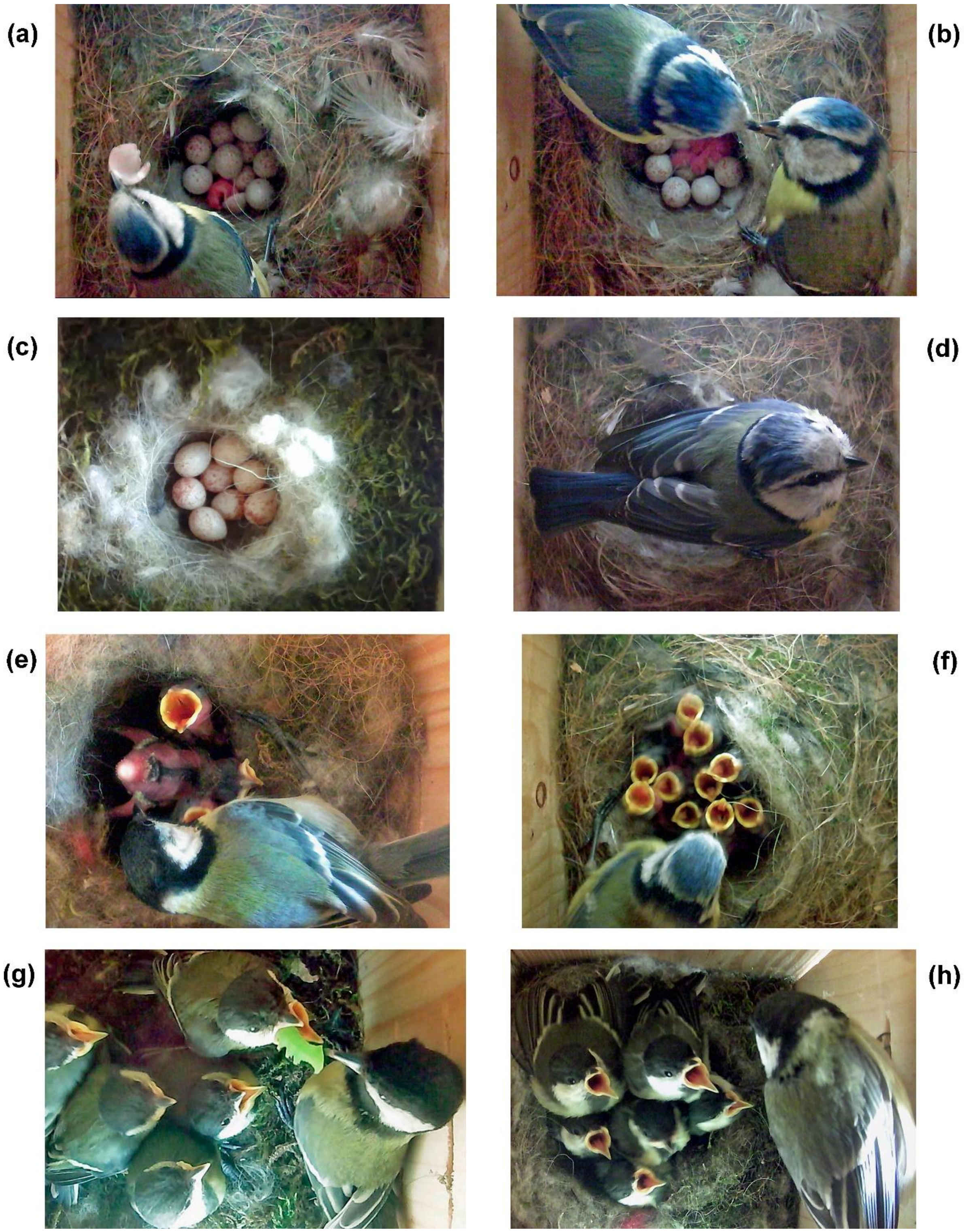
(o)

(p)

(q)

(r)

Figure 6. Examples from videos recorded by the Internet-connected Smart Nest Box (SNBox): Snapshot of (a) a Eurasian Blue Tit (*Cyanistes caeruleus*) parent removing eggshell of the hatchling; (b) Eurasian Blue Tit parents with the clutch and hatchlings; (c) a clutch of Great tit (*Parus major*); (d) a Eurasian Blue Tit parent; (e) a Great Tit parent removing droppings of the hatchling; (f) Eurasian Blue Tit nestlings with a parent; (g–h) a Great Tit parent feeding the nestlings; (i) a Common Redstart (*Phoenicurus phoenicurus*) male feeding the incubating female; (j) a Common Redstart female with the clutch; (k) a Great Tit female defending the clutch; (l) the sleeping Great Tit female; (m) Common Startling (*Sturnus vulgaris*) hatchlings; (n) a parent of Common Starling feeding the nestlings; (o–p) a parent of Common Starling with the begging nestlings; (q) a Great Spotted Woodpecker (*Dendrocopos major*) individual; (r) courting Common Swifts (*Apus apus*); (s) parents of Eurasian Tree Sparrow (*Parus montanus*) with the nest material; (t) American Red Squirrel (*Tamiasciurus hudsonicus*) young; (u) a Carolina Wren (*Thryothorus ludovicianus*) individual; (v) a Flying Squirrel (*Glaucomys* sp.) individual; (x–y) a Little Owl (*Athene noctua*) male delivering (x) an Earthworm (Oligochaeta) and (y) an *Apodemus* prey.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2.5 Conclusion

I have highlighted the uses of nest boxes for the purposes of avian research, and the uniqueness of their use in combination with technical devices. Nest boxes mainly facilitate accessibility to bird nests. This advantage has been frequently used for collecting biological data on insectivore bird species, but also for monitoring species that would otherwise be difficult to study, such as owls. Additionally, with their ample inner space, water resistance, and steady location, nest boxes provide great conditions for fitting various technical devices for the purposes of indirect observation, and it makes them a unique tool for advanced data acquisition.

Although technical devices mounted within nest boxes facilitate data collection, they differ substantially in their quality and cost, with the main choice to be made between off-the-shelf devices and purpose-designed systems. In this respect, I have reviewed the extensive use of off-the-shelf technical devices on the one hand and pointed out the under-appreciated potential of recently used technologies on the other hand. To document this, I have introduced and described our own purpose-designed camera system — available as the stand-alone and Internet-connected Smart Nest Boxes (SNBoxes) — that we have designed, developed and applied. The use of such systems provides potential to enhance ornithological and ecological research, but in particular it allows us to: (i) extend the range of research objectives in time and space; (ii) choose technical devices and sensors to match specific research objectives; (iii) collect specific information on animal behaviour (e.g., prey delivery) without trigger delay; (iv) achieve efficient collection, management, and dissemination of a large volume of data; and (v) apply the reliable use of these systems under various weather conditions. This approach, with all its technical facilities, even exceeds research objectives. In particular, it provides benefits for formal and informal education and allows to engage the public into research activities. I will document these claims below, in Chapter 3 (research benefits) and 4 (educational benefits).

3 Using Automated Data Collection for Behavioural Ecology Research

Case study: Does the small male hypothesis apply to Boreal Owls?

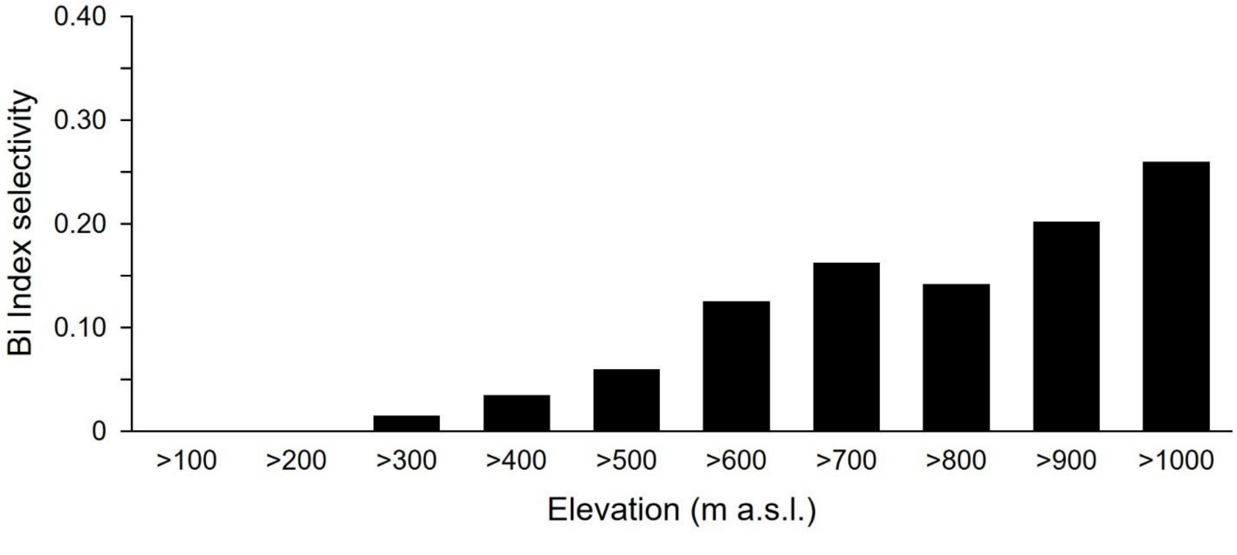
In this chapter, I document an example of using purpose-designed systems to enhance ornithological research through gathering unique data on the dietary ecology of the Boreal Owl. I use the dataset obtained from our stand-alone SNBoxes (for details, see Chapter 2.4) used in the nest box population of Boreal Owls in the Ore Mountains, Czech Republic. I first introduce the general patterns of the behavioural ecology of Boreal Owls (Chapter 3.1), before then turning my attention to describe the "small male hypothesis" (Chapter 3.2.1) that I will test (Chapter 3.2.1). Using four SNBoxes, we sequentially replaced the original nest boxes during 41 nesting attempts in 2014–2017 (Chapter 3.2.2) to record all prey items delivered by the male and female parents to their nestlings. Based on manually evaluating video contents, I obtained a unique dataset on the type and handling of 5491 prey items provided by the males during 888 nights. In this dataset, I identified 99% of all prey to the species, genus, or class level, as well as I identified the body part of the delivered prey (e.g., delivering decapitated prey) and the age of bird prey (adults vs nestlings) (for details, see Table 2). For the purposes of testing the hypothesis, I combine the dataset obtained by the SNBoxes with measured data on body mass and wing length of the Boreal Owl males, body mass of prey items stored in owls' nests, and trapping data on the abundance of small mammal prey (Chapter 3.2.2). To the best of my knowledge, such detailed dataset has never before been available in any study of any species to examine the selective forces that have resulted in reverse sexual dimorphism in birds.

3.1 A review of Boreal Owl ecology

3.1.1 Distribution and habitat used

The Boreal Owl is a cavity-dwelling species that occupies, in five subspecies, the circumpolar Holarctic area across the boreal coniferous forests of Eurasian and North American, and reaches high-elevation subalpine forests further south (König and Weick 2008). The distribution of *Aegolius funereus funereus* in Europe corresponds with the natural distribution of Norway Spruce (*Picea abies*), and local populations also occur in high-elevation coniferous forests in southern Europe (Vrezec 2003, Lopéz et al. 2010). In the Czech Republic (hereafter also Czechia), the Boreal Owl inhabits coniferous (including non-native Blue Spruce, *Picea pungens*) forests rather than deciduous and mixed forests (Šťastný et al. 2006, Zárybnická et al. 2015d), and this preference can change over the process of tree leafing (Zárybnická et al. 2017c). The occurrence of this owl increases with increasing elevation, showing a preference for altitudes above 600 m a. s. l. in Czechia, which is the highest elevation preference for any species of Czech owls (Fig. 7, Zárybnická et al. unpublished data, Zárybnická et al. 2017b). This narrow habitat selectivity is in accordance with the high level of specialization of Boreal Owl reported by Morelli et al. (2019), indicating the potential risk for this species in the face of changes to land use and climate (Julliard et al. 2006).

Figure 7. The preferences of the Boreal Owl for elevational bands in Czech Republic, calculated using the standardized Bi Manly's index (*n* = 604 squares) and tested using linear regression (F = 126.0, $\beta = 0.970$, P < 0.0001, *n* = 114 occupied squares) (Zárybnická et al. unpublished data). The data used here were extracted from the Atlas of birds breeding in the Czech Republic in 2001–2003 (Šťastný et al. 2006).



3.1.2 Nest box occupancy and the use of automated monitoring

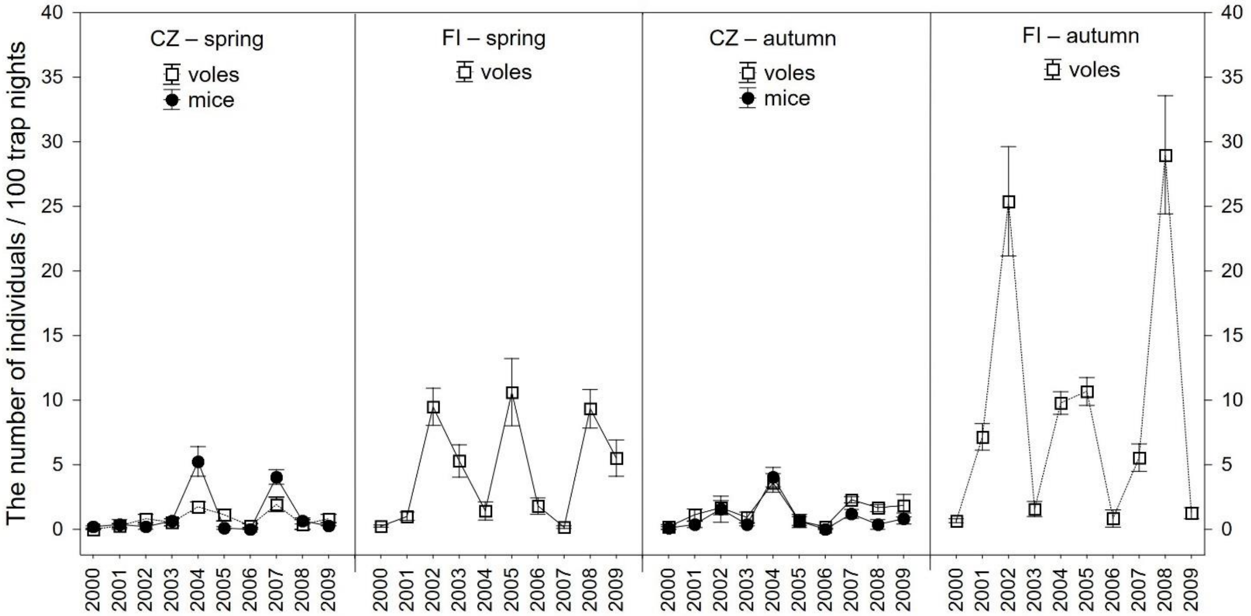
The Boreal Owl does not build its own nest, apart from scraping a shallow dent in the soft material at the bottom of the tree cavity. In Eurasian coniferous habitats, this forest specialist mainly depends on cavities excavated by Black Woodpecker (*Dryocopus martius*), which produces tree cavities that are sufficiently large for the Boreal Owl. If the population of this keystone species declines, then many secondary cavity users, including the Boreal Owl, will decline along with it (Korpimäki and Hakkarainen 2012, Mikusiński et al. 2018). However, the Boreal Owl readily uses nest boxes to breed, which are effective substitutes for natural cavities (Drdáková-Zárybnická 2003, 2004, Korpimäki and Hakkarainen 2012). The willingness of the Boreal Owl to occupy nest boxes makes this owl a “textbook example” of a species whose breeding biology and dietary ecology have been primarily discovered based on studies of nest-box-using populations (e.g., Scherzinger 1970, Schelper 1972, Korpimäki 1981, Sonerud 1985a, b, Hörnfeldt et al. 1988, Hayward et al. 1993, Mezzavilla et al. 1994, Korpimäki and Hakkarainen 2012, Zárybnická et al. 2013, Rajković 2018). Moreover, nest boxes enable camera systems and various sensors to be mounted for the purposes of nest monitoring and obtaining data that would otherwise be difficult or impossible to study. The first studies using automated electromagnetic circuits to record the activity patterns of breeding Boreal Owls were conducted in the 1970s by Klaus et al. (1975) and Korpimäki (1981). Since then, various camera systems have been designed, developed, and applied for Boreal Owl nests by our group within the research that I have initiated and directed since 2002 (Bezouška et al. 2005, Drdáková-Zárybnická 2008, Zárybnická 2009b, a, Zárybnická et al. 2009, 2011, 2012, 2016, Zárybnická and Vojar 2013, Kouba et al. 2014b, 2015, Šindelář et al. 2015), as well as in the research of other groups (Slagsvold and Sonerud 2007, Sonerud et al. 2014b, Sørås et al. 2019).

3.1.3 Geographic trends in trophic characteristics of birds of prey

The most abundant prey of most raptors and owls in the western Palearctic consists of small rodents (Newton 1979, König and Weick 2008), and the level of diet specialization increases with latitude (Korpimäki and Marti 1995). In northern Europe, voles of the genera *Microtus* (most commonly the Field Vole *M. agrestis*, the Tundra Vole *M. oeconomus*, and the Common Vole *M. arvalis*) and *Myodes* (most commonly the Bank Vole *M. glareolus*) are the dominant prey of most birds of prey, and their proportion in diets is usually closely related to their availability in the wild (Korpimäki 1985, 1986b, a, 1988, Sonerud 1986, Korpimäki and Sulkava 1987, Korpimäki et al. 1990, Jacobsen and Sonerud 1993, Solonen et al. 2017). At higher latitudes, voles undergo regular three- or four-year cycles (Fig. 8, Zárybnická et al. 2015e), with considerable multi-annual and intra-seasonal changes in abundance, whereby high peaks of vole abundance tend to be followed by population crashes typically start in early spring and continue throughout the summer (Hansson and Henttonen 1985, Norrdahl 1995, Krebs 2013).

Microtus voles are also important prey for birds of prey in temperate areas, such as Czechia, but they tend to be a stable source of food (e.g., Pokorný et al. 2003, Zárybnická et al. 2013, Zárybnická et al. 2017b), resulting from relatively stable within- and between-year abundances, exhibiting only moderate and irregular seasonal changes (Hansson and Henttonen 1985, Hanski et al. 1991, Krebs 2013, Zárybnická et al. 2015e, 2017a; Fig. 8). Also, the diet of avian predators in temperate areas is enriched with other prey species, mainly *Apodemus* mice (Village 1990, Alivizatos and Goutner 1999, Obuch 2011, Zárybnická et al. 2011, 2013, 2017b, Luka and Riegert 2018, Riegert 2018) that may undergo regular three-year cycles while the cyclicity of *Microtus* voles may be absent (Zárybnická et al. 2015e, 2017a, Fig. 8). Farther south, even more prey species, such as the genera *Mus*, *Meriones*, *Gerbillus*, *Crocidura*, and *Suncus*, enrich the diet of birds of prey (Goutner and Alivizatos 2003, Obuch and Benda 2009, Šindelář 2012, Obuch 2018).

Figure 8. Population dynamics of *Microtus* voles and *Apodemus* mice in Czechia and Finland during spring and autumn in 2000–2009. Means ± SD are shown. For details, see Zárybnická et al. (2015e).



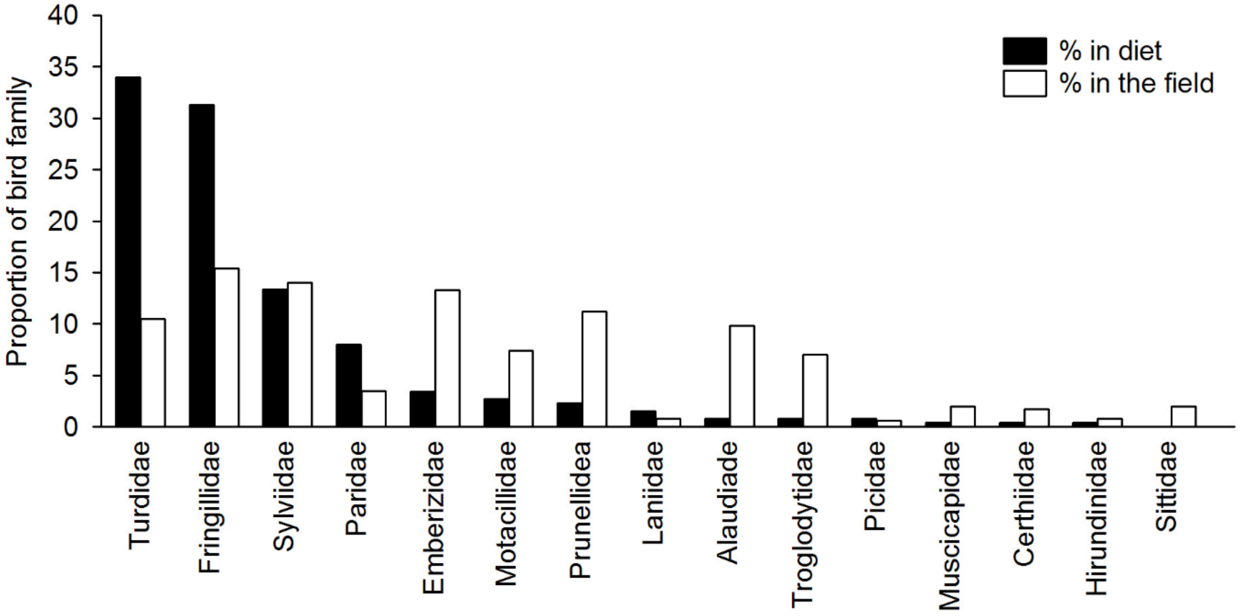
3.1.4 Response of the opportunistic Boreal Owl to changing food supply

Birds of prey show both numerical and functional responses to the multiannual changes in the availability of their preferred prey. As a numeric response, birds move to another area when food is rare (Mikkola 1983, Korpimäki 1984b, 1986b, Sonerud et al. 1988, Poulin et al. 2001), and this response has been mainly found in northern latitudes where most vole-eaters have adapted to large vole fluctuations by becoming nomadic (Korpimäki 1994, Poulin et al. 2001). In central Europe, where irregular and moderate vole cycles have been reported and the diet is enriched by other prey (see above), these relationships are not as pronounced and other factors (e.g., winter climatic conditions; Kostrzewa and Kostrzewa 1991) may also influence the population densities of birds of prey. Regardless of geographical area, most opportunistic predators, including the Boreal Owl, also show strong functional dietary responses to low availability of their preferred prey. Mainly, they reduce consumption of their dominant prey and increase consumption of alternative prey, resulting in an increased diversity in their diet (Korpimäki 1988, 1992, 1994, Steenhof and Kochert 1988, Zárybnická et al. 2011, 2013, 2017b).

The opportunistic Boreal Owl basically feeds on *Microtus* voles in northern areas and *Microtus* voles and *Apodemus* mice in temperate regions, respectively (Korpimäki 1988, Pokorný et al. 2003, Zárybnická et al. 2011, 2013, 2017b, Korpimäki and Hakkarainen 2012). The rate of consumption of this prey relates to their availability in the field (Korpimäki 1988, Jacobsen and Sonerud 1993, Zárybnická et al. 2013), although it may not be the case for *Microtus* voles when *Apodemus* mice is abundant (Zárybnická et al. 2013). Boreal Owls adjust their breeding densities according to the abundance of preferred (hereafter also *main*) prey (Korpimäki 1981, Korpimäki and Hakkarainen 2012), but this numeric response may not apply in temperate areas (Zárybnická et al. 2013, 2015e). Most importantly, Boreal Owls have adapted functional responses to changing food conditions. Mainly, when *Microtus* voles and *Apodemus* mice are scarce, both northern and temperate Boreal Owl populations switch to alternative prey, mainly *Sorex* shrews (Common Shrew *S. araneus* and Eurasian Pygmy Shrew *S. minutus*) and birds (Korpimäki and Hakkarainen 2012, Zárybnická et al. 2013, 2017b). This shift is usually associated with a drop in reproductive success and influences other breeding characteristics (for details, see below).

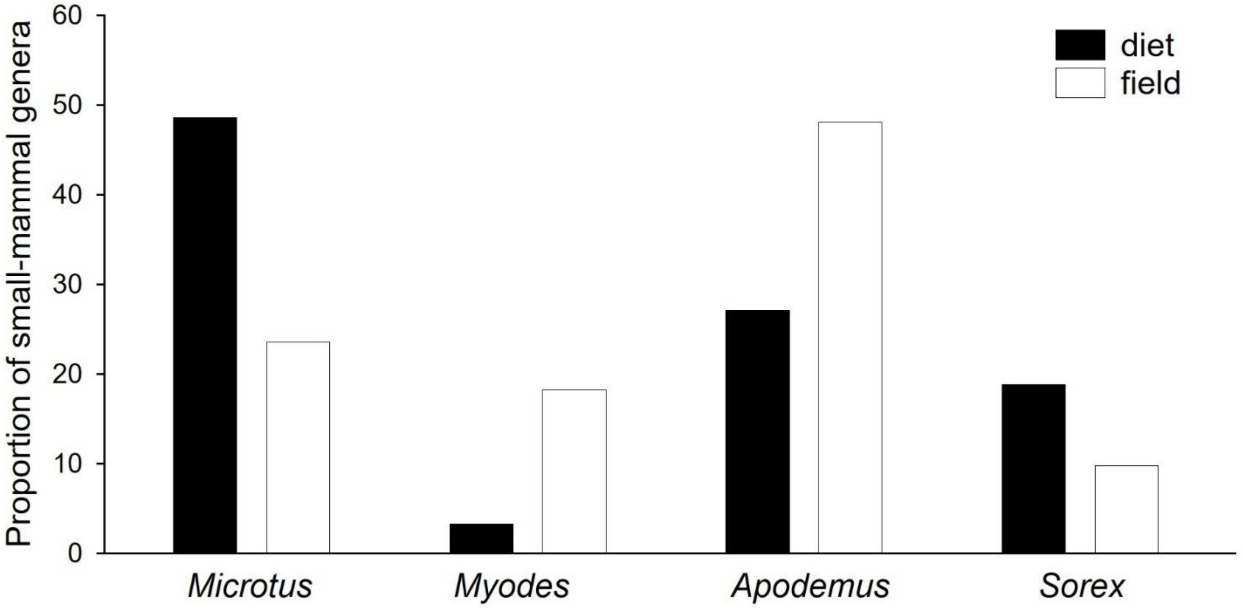
As noted above, *Sorex* shrews and birds are typical alternative prey of the Boreal Owl: while shrews provide reduced amount of energy because of their small body size (Zárybnická et al. 2009), birds are more challenging to search for and more difficult caught than mammal prey (Temeles 1985, Hakkarainen and Korpimäki 1991). On average, birds comprise 7.5% of the Boreal Owl diets by numbers and 9.5% by mass, but they can represent about 33% of Boreal Owl diets by numbers and up to 50% by mass when small mammals are scarce (Korpimäki and Hakkarainen 2012). More than 60 bird species have been found in the diet of the European Boreal Owl, with the main ones being finches (Fringillidae), thrushes (Turdidae), tits (Paridae), Yellowhammers (*Emberiza citronella*), Bullfinches (*Pyrrrhula pyrrhula*), and leaf warblers (*Phylloscopus* spp.) (Korpimäki and Hakkarainen 2012, Zárybnická et al. 2013). Additionally, I have found that the Boreal Owl prefers to hunt the most available birds, although thrushes (Turdidae), finches (Fringillidae) and tits (Paridae) have been exploited disproportionately more often than would be indicated by the relative sizes of their populations in the field (Fig. 9., M. Zárybnická unpublished data). Apart from adult individuals of bird prey, it is likely that Boreal Owls also search for and feed on the nestlings of other bird species. However, because of methodological difficulties, little is known about foraging strategies of this owl species, including the proportion of bird nestlings and adults in the owl's diet, the frequency of and reasons for prey decapitation, the level of energetic expenditure required to hunt different types of prey, as well as the differences in hunting strategies between sexes.

Figure 9. Proportions of bird families in the diet of Boreal Owl and their availability in the field (%) in the Ore Mountains, Czech Republic, in 1999–2010 (M. Zárybnická, unpublished data). The data used here were collected in the field (the abundances of bird families) and based on pellet's analyses of the owls' diet.



Compared to other prey groups, the role of Bank Voles in the owls' diet is more disputable. In northern areas, this vole species has usually been considered as the most important alternative prey of the Boreal Owl (Korpimäki 1988, Korpimäki and Norrdahl 1989). Compared to *Microtus* voles, multiannual cyclic fluctuations of Bank Vole are not so evident (Korpimäki 1988, Korpimäki and Norrdahl 1991, Korpimäki et al. 1991). Also, this vole species usually represents lower numbers in the owl diet compared to *Microtus* voles (Korpimäki 1988, Jacobsen and Sonerud 1993, Norrdahl and Korpimäki 2002, Norrdahl et al. 2004), and there may be less of a link between the proportion of Bank Vole in the owl diet and its abundance in the field (Korpimäki 1988, Korpimäki et al. 1990, Korpimäki and Norrdahl 1991). Finally, the relationship between the abundance of Bank Vole in the field and reproductive output and breeding density of the owls may be weaker than with *Microtus* voles (Korpimäki 1984b, 1992, Korpimäki and Norrdahl 1991). It has been suggested that *Microtus* voles are taken by Boreal Owls more often than Bank Voles because of *Microtus* voles, mainly Field Voles, move more slowly and being more easily caught than the more agile Bank Voles (Jacobsen and Sonerud 1993). Moreover, Field Voles are heavier and energetically more profitable in size than Bank Voles (Korpimäki and Norrdahl 1989), and the rate of encountering Field Voles in open areas is usually higher than that with Bank Voles in forests (Jacobsen and Sonerud 1993, Hakkarainen et al. 2003). Additionally, Bank Voles (as well as *Apodemus* mice) show great scansoriality, i.e., the ability to climb trees up to 5 m (Holíšová 1969, Montgomery 1980, Tattersall and Whitbread 1994), which may make this prey more difficult to hunt for the owls. As a result, Bank Voles comprise the most important alternative prey of Boreal Owls in northern areas, but because of a broader range of prey species further south, Bank Voles may be less often hunted by temperate Boreal Owl populations (Fig. 10). This would be consistent with the lack of impact of this vole prey on the reproductive output of the owls in temperate areas (Zárybnická et al. 2013, 2015a).

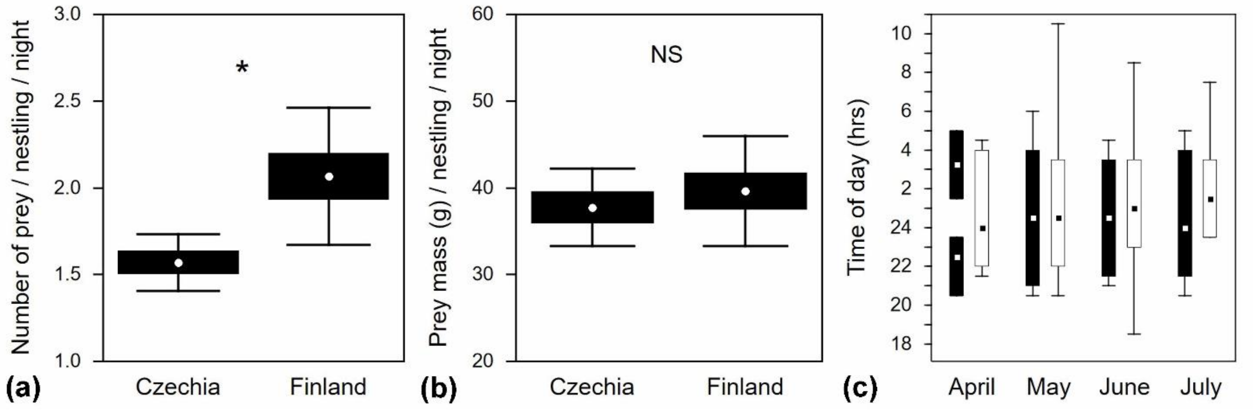
Figure 10. Proportions of small mammal groups in the diet of the Boreal Owl and in the field in the Ore Mountains, Czech Republic, in 1999–2010. For further details, see Zárybnická et al. (2013).



3.1.5 Reproductive patterns under various environmental conditions

Environmental conditions, and mainly the food availability changing over time and space, influence the reproductive and life-history strategies in birds of prey (Newton 1979), and these relationships have been frequently documented in the Boreal Owl. More specifically, the abundance of the preferred prey (*Microtus* voles and *Apodemus* mice, see above) affects many aspects of breeding biology of this owl, for instance: breeding density and laying date (Korpimäki and Norrdahl 1989, Korpimäki and Hakkarainen 2012); vocal activity of adults (Ševčík et al. 2019); clutch size and fledgling productivity (Korpimäki 1987, Korpimäki and Hakkarainen 2012, Zárybnická et al. 2015e); the predation rate of owls' nests (Zárybnická et al. 2015c), provision rate, brooding bout duration, and nest desertion rate (Eldegard and Sonerud 2009, 2010, 2012, Zárybnická 2009b, Zárybnická et al. 2009, 2012); sex allocation (Hipkiss and Hörnfeldt 2004, Schwerdtfeger and Wink 2014); nestling fitness (Zárybnická et al. 2015b), begging intensity of fledglings (Kouba et al. 2014a); and breeding home range size (Kouba 2009, Kouba et al. 2013). Reproductive strategies can also change over geographic areas under different environmental conditions. For example, as shown in Fig. 11, high within-season vole fluctuations during late spring and early summer accompanied by short nights and limited time for foraging can lead to higher hunting effort, increased nestling mortality, and poor reproductive success in Finish owls, whereas Boreal Owl populations in temperate areas face high nest predation rates from Pine Martens (*Martes martes*) and gain from the relatively stable and more diverse prey community and longer nights for foraging (Zárybnická et al. 2009, 2012, 2015c, 2015e).

Figure 11. Differences in provision effort of northern and temperate Boreal Owl males resulting from variability in food availability and the time for foraging (i.e., length of the night) collected by a preliminary model of Smart Nest Boxes used in 2004–2006 in Czechia and Finland (for details, see Zárybnická et al. 2009, Zárybnická et al. 2012). Significant differences in species composition of prey provided by the males for their nestlings at the two study sites have been found: mostly, *Apodemus* mice (58.6%) and *Microtus* voles (26.1%) were delivered by the Czech males to their nestlings; whereas, *Microtus* voles, Bank Vole (61.5%), and *Sorex* shrews (27.6%) were provided by the Finnish males. As a result, the Czech males provided (a) lower numbers of (b) heavier prey during (c) longer foraging times (black columns), while Finnish males delivered (a) higher numbers of (b) lighter prey during (c) shorter foraging times (white columns).



3.2 Testing of the small male hypothesis

3.2.1 Introduction to the small male hypothesis

Opportunistic foraging behaviour documented in the Boreal Owl (see Chapter 3.1.4) is consistent with the theory of optimal foraging, which assumes that animals should take the most economically advantageous foraging pattern under the given constrains of environments when searching for food (Emlen 1966, MacArthur and Pianka 1966, Schoener 1971, Charnov 1976). More specifically, the optimal foraging behaviour should provide the greatest net benefits for the lowest costs, and it should be considered in relation to optimal prey size and the expense in terms of time and energy required for searching, handling, eating, and transporting the prey (Charnov 1976, Stenseth and Hansson 1979, Sih and Christensen 2001, Davies et al. 2012), which is the most critical aspect at the time of providing for nestlings. Adopting advantageous foraging strategies will, as a result, increase the survival and reproductive success of individuals, and therefore should be favoured by natural selection (Darwin 1859, Davies et al. 2012).

In birds of prey, foraging strategies greatly differ among species (Reynolds 1972, Andersson and Norberg 1981, Olsen 1987, Krüger 2005, Riegert 2018), the sexes (Newton 1979, Mueller 1986, Shine 1989, Sergio et al. 2007) and even individuals (Hakkarainen and Korpimäki 1991, Sonerud 1992, Hakkarainen et al. 1996, Sørås et al. 2019). Body size of avian predators influences their foraging strategies and hunting success, insofar as smaller predators will be more agile, require less power for flight, and, as a result, forage more efficiently (Norberg 1970, Pennycuick 1975, Witter and Cuthill 1993). Related to this, a broadly accepted hypothesis — *the small male hypothesis* — suggests that the foraging efficiency of small males and the reduced competition for food between small males and larger females have led to the evolution of reversed sexual size dimorphism in birds of prey (Selander 1966, Storer 1966, Reynolds 1972, Lundberg 1986, Ydenberg and Forbes 1991). This hypothesis has been also supported by small number of observational and experimental studies (Hakkarainen and Korpimäki 1991, Hakkarainen et al. 1996, Massemin et al. 2000).

However, data on foraging and provision efficiency is difficult to collect, and therefore studies providing evidence for the small male hypothesis are rare, especially in nocturnal owls. Even when such studies have been conducted, they have often suffered from several methodological weaknesses. First, it is unclear if body size — expressed as body mass or skeleton size, or both — is related to foraging strategy. Some of the studies have even excluded body mass from consideration and only used wing length or other structural measurements (Storer 1966, Paton et al. 1994, Massemin et al. 2000, Krüger 2005, McDonald et al. 2005). Second, most of the studies has not considered in their analyses that — body mass and skeleton size — differ substantially in their variability over time. While body mass can change rapidly depending on daily energy budget and vary greatly throughout the nesting phase, breeding season, and between years (Newton 1979, 1983, Dijkstra et al. 1988, Korpimäki 1990, Hakkarainen and Korpimäki 1993, Pietiainen and Kolunen 1993, Hipkiss 2002), skeleton size is usually relatively stable or change only moderately over time (e.g., wing length may be shortening between moulting cycles; Pienkowski and Minton 1973). Third, some studies have used indexes that combine skeleton and body mass measurements (Hakkarainen and Korpimäki 1991, Hakkarainen and Korpimäki 1995), but such approach may remove the measure of size from any clear function. Fourth, the foraging efficiency of avian predators has often been expressed indirectly through the structure of prey (usually based on literature sources; Storer 1966, Krüger 2005) or reproductive parameters such as clutch size or fledgling productivity (Hakkarainen and Korpimäki 1991, Massemin et al. 2000, McDonald et al. 2005, Sergio et al. 2007, Perez-Camacho et al. 2015). There are very few studies that have expressed the feeding efficiency of bird individuals as the number of prey items delivered to the nestlings (provisioning rate or prey delivery rate), and if such studies exist, they have conducted their measurements either in laboratory conditions (Hakkarainen et al. 1996) or based on personal observations during a limited period of the night and the nestling period (Hakkarainen and Korpimäki 1995).

Below, I test and verify the small male hypothesis in the Boreal Owl population occupying nest boxes in the study area in central Europe (the Ore Mountains, Czechia). Specifically, I hypothesise that smaller males (i.e., males with smaller wing length) or lighter males (i.e., males with lower mass for their skeletal size), or both, will provide (i) more prey items to produce more nestlings or, alternatively, (ii) lower numbers of energetically advantageous food (heavier prey) to raise the same or higher number of nestlings compared to larger or heavier males. Simultaneously, I hypothesise that (iii) smaller males or lighter males, or both, will be more successful in providing bird prey, that is more frequently preyed upon when the owls' main food is scarce, and these males will produce more nestlings than their larger and heavier counterparts. For the purposes of testing the hypotheses, I combine the dataset obtained by the SNBoxes installed at 41 Boreal Owl nests between 2014 and 2017 with measured data on body mass and wing length of Boreal Owl males, body mass of stored prey in owls' nests, and trapping data on the abundance of small mammal prey.

3.2.2 Methods

Study area and study population

The study was carried out in a Boreal Owl population breeding in nest boxes between 2014 and 2017 in Czechia. The study site was situated in the Ore Mountains, close to the border with Saxony (50.6°–50.7°N, 13.5°–13.8°E) at elevations from 730 to 960 m a. s. l., covering 100 km^2. This area consists a specific habitat that had resulted from significant impacts of air pollution during the second half of the 20th century, followed by intensive logging of dead trees and a restoration process hindered by the high acidity of the soil, harsh mountain weather, and extensive damage to young plantations caused by cervids (Kopáček and Veselý 2005, Hruška et al. 2009). The habitat of the current landscape is characterized by a mosaic of small patches of native Norway Spruce (*Picea abies*) forests, secondary stands dominated by non-native Blue Spruce, and open areas with solitary European Beech trees (*Fagus sylvatica*) with a ground cover dominated by *Calamgrostis villosa* (for details, see Zárybnická et al. 2015d).

In the study site, Boreal Owls breed primarily in nest boxes (> 90%), as natural cavities are mostly confined to rare solitary European Beeches. The owls usually breed from late March to July, and a full nest cycle takes about two months (26–32 days of incubation and 27–38 days of brooding; Drdáková-Zárybnická 2002, Kouba et al. 2014b, Zárybnická et al. 2015b). The females incubate their eggs and brood hatchlings almost continually, and they only leave their nests for a few minutes every night in order to defaecate, regurgitate the remains of food, and preen (Zárybnická unpublished data, Zárybnická et al. 2009). The males provide essentially all food for their mates and young from egg-laying (Zárybnická et al. 2009, 2012, M. Zárybnická unpublished data) to independence of the fledglings (i.e., 5–9 weeks after fledgling, Eldegard and Sonerud 2009, Eldegard and Sonerud 2012, Kouba et al. 2013). If the male owls fail to provide food for their families during the incubation or early nestling phase, then the females abandon their clutches and broods, and nesting attempts fail (Zárybnická and Vojar 2013).

During 2014–2017, we deployed and regularly checked 212–246 (mean ± SD, 234.3 ± 16.0 per year) standard wooden nest boxes (for details, Drdáková-Zárybnická 2002), in which we found a total of 86 Boreal Owls' nests (21.5 ± 9.9 per year). We checked all nests once per week to collect the information on clutch size, brood size, and to identify and weigh stored prey (n = 527 individual prey items). We also trapped the male owls when they delivered prey to their nests to measure the maximal length of the owl's wings and weigh their body mass (for details, see Table 1).

Small mammal abundance

The abundance of small mammals in the field was assessed using snap traps. Trapping was carried out at the beginning of June each year from 2014 to 2017 by setting up snap traps (baited with wicks roasted in a mix of bacon and flour) in three one-hectare areas (100 × 100 m squares; 11 × 11 trap grid; 10-m span, 121 traps in total for each square). The traps were left out for three days and checked every morning and reset whenever closed. All captured mammals (n = 120) were identified to species level and grouped according to the genera: i.e., *Apodemus* mice (Yellow-necked Mouse and Wood Mouse), *Microtus* voles (Field Vole and Common Vole), *Myodes* voles (Bank Vole), and *Sorex* shrews (Common Shrew and European Pygmy Shrew) (for details, see Zárybnická et al. 2013). I calculated the abundance of each prey group as the mean number of captured individuals per hectare (trapping site) summed over three trapping nights.

SNBox application and data extraction

For the purposes of Boreal Owl nest monitoring, my colleagues and I sequentially reused four SNBoxes to replace existing nest boxes in randomly chosen ongoing nesting in 2014–2017 (for details, Table 1). The process required finding active owl nesting in regular nest boxes and then replacing them with SNBoxes (for details, see Chapter 2.4.3). After collecting all the video data, we automatically extracted contextual data (e.g., date and time) and manually evaluated the biological information from the audiovisual data (for details, see Chapter 2.4.4). For the purposes of testing the small male hypothesis, I have analysed and evaluated the data on the composition of prey provided by the male owls for their nestlings and mates. I included the data from a total of 41 nesting attempts of 33 males that we caught, ringed, aged, and measured to gain the necessary information on wing length and body mass (Table 1). While 28 males provided for their nestlings at only one nest, five males were recaptured: three of them provisioned the nestlings at two nests in two different years; one provisioned at three nests in three years; and one provisioned at four nests in four years. During 888 nights (monitored between 17 April to 20 August), the males delivered to their 192 nestlings a total of 5491 prey items that I identified to species, genus, or class level and sorted into six groups: *Microtus* voles (*Microtus* sp.), *Apodemus* mice (*Apodemus* sp.), *Myodes* voles (Bank Vole), *Sorex* shrews (*Sorex* sp.), birds, and other prey (Hazel Dormouse *Muscardinus avellanarius*, unidentified mammals, and invertebrates). I also identified the manner with which the male owls delivered prey to their nestlings, and the completeness of the prey, i.e., whole prey, decapitated prey, only the head, or the rest of the prey (for details, see Table 2).

Table 1. The characteristics (mean, SD, minimum, maximum) of Boreal Owl nest monitoring using four SNBoxes applied in 41 nesting attempts during 2014–2017 in the Ore Mts., Czechia, along with measurements of body mass and wing length of the male owls (*n* = 41 males, including recaptured males).

Nest characteristics and male owl measurements	Mean	SD	Min	Max
No. of nests monitored by SNBoxes / year	10.3	5.4	6	18
No. of nights monitored by SNBox / nest	21.7	10.0	2	37
No. of determined prey items / nest	133.9	63.5	8	258
No. of nestlings / nest	4.7	1.7	1	8
Nestling age / nest	19.1	5.2	1	37
Wing length of males (mm)	164.0	5.7	151	178
Body mass of males (g)	104.1	5.6	92	118

Statistical analyses

For the analyses, I treated the data from each night as a separate data point (*n* = 888 male-nights) recording the number of prey items provided by the males (hereafter *provisioning rate* or *prey delivery rate*). In addition to the data from the SNBox cameras, I have used annual measurements (carried out during the breeding season) of body mass and wing length of the male owls, and indices of the abundance of separate small mammal groups from trapping. Although each male was only measured once each year (breeding season), body size of bird of prey males can vary through time, with mass potentially varying substantially even over the course of a single nesting attempt (Dijkstra et al. 1988) Thus, I needed to account for within-male variation in size, which I did by calculating residuals of both body mass and wing length after regressing measures of these traits against calendar day of size measurement, reproductive day of size measurement, and year (as a categorical variable). These residuals describe the size of each male relative to all other males in the population in a given year, and so I examined whether relatively small males performed better than relatively large males. As natural selection on body size will have operated on relative sizes of males, my use of these residuals of body size measurements is appropriate.

To test the small male hypothesis, I used two Generalized Linear Mixed Models (GLMMs). First, I used a GLMM with a negative binomial error distribution to identify predictors of provisioning rate; the response data were positive integers (i.e., counts of items delivered); over-dispersion of these counts indicated that a negative binomial model was more appropriate than a Poisson regression. I tested for the existence of relationships between provisioning rate and the following fixed effects (predictors): residuals of body mass, residuals of wing length, number of nestlings being provisioned, nestling age, calendar day (i.e., days since 1 January), and abundance of the main prey (i.e., *Apodemus* mice and *Microtus* voles). I did not include my indices of *Sorex* shrew and *Myodes* voles (Bank Vole) abundance from the fixed effects because they positively correlated with *Apodemus* mice and *Microtus* voles, respectively; further, preliminary analyses showed that models were unstable — failing to converge, or substantially changing results in biologically unreasonable ways — when either of these indices of *Sorex* shrew or *Myodes* vole abundance were included as predictors. In addition to the main effects tested, I included three biologically relevant interactions in the analysis: residuals of body mass × residuals of wing length; the number of nestlings provisioned × residuals of body mass; and the number of nestlings provisioned × residuals of wing length. I also included the ring ID of each individual male as a random factor (I did not include the year as a random effect because its effect in the logistic model was not significant). Second, I used a set of logistic regression models (i.e., GLMMs with binomial error distribution) to assess the proportion of separate prey groups — *Apodemus* mice, *Microtus* voles, *Sorex* shrews, *Myodes* voles, and birds (I performed five analyses) — in the total Boreal Owl diet (including *other prey*) in which the proportion of prey deliveries of each focal prey group at a site on a given night was modelled; these models describe the probability per night of any member each of these groups of prey being delivered to a nest. I modelled these probabilities as a function of the residuals of body mass (*hereafter* body mass), residuals of wing length (wing length), provisioning rate, the number of nestlings provisioned (brood size), nestling age, calendar day, and abundance of the main prey in that year (i.e., *Apodemus* mice and *Microtus* voles). Similar to the first analysis, I included three biologically relevant interactions in this analysis — residuals of body mass × residuals of wing length; brood size × residuals of body mass; and brood size × residuals of wing length — as well as ring IDs of males as a random factor (the effect of the year was not significant in the logistic model). I used a P-value of < 0.05 to indicate the statistical significance of fixed effect and related interactions. I also counted confident limits for all predictors. All models were fitted using restricted maximum likelihood implemented with the *glmer* function from the *lme4* package (Bates et al. 2012) within R (version 3.6.1; R Development Core Team 2013).

I did not use any procedure, such as AIC-based multi-model inference or stepwise regression, in order to identify a “best” set of predictor variables to include in the models that I am presenting. The purpose of my analyses was to test a set of hypotheses, and each predictor variable in a model represents either a hypothesis to be tested or is a known predictor of variation in the responses examined. As such, the appropriate statistical tool is the fitting of a single model for each response variable, followed by assessing the statistical importance of relevant predictors using P-values or similar metrics (such as confidence limits). In contrast, multi-model inference using AIC scores has a different purpose of identifying combinations of predictor variables that yield accurate predictions from independently collected data regardless of whether the best-predicting model excludes biologically important predictor variables, and step-wise regression has no theoretical basis for claiming to identify all important predictors (Burnham and Anderson 2002).

To visualize the patterns described by these models, I produced figures for significant relationships between explanatory variables (provisioning rate, proportions of separate prey groups) and responses, or the interactions of two predictors. To show the specific effects of the models, I created a set of fake data in which all predictor values had a constant value except for the predictor(s) of interest (i.e., the significant ones), which were systematically varied as sequences of values between the minimum and maximum observed values for these variables. Then, I identified the most typical category in the random effect (i.e. the ring number for which the random effect coefficient was closest to zero). I then used the function *predict* with its *newdata* argument in order to calculate the predicted values for each record in the fake data, with these predicted values being subsequently plotted on graphs. To show the relationship between the explanatory variable and the interaction of two predictors (additional effect), I plotted one of the changing predictor variables along the x-axis and, for the other predictor variable, plotted three lines fitting the 10th quantile, median, and 90th quantile of the second predictor's values. For producing the figure between an explanatory variable and a significant predictor, I applied the same procedure as for the interaction of two predictors but I calculated the set of fake data with only one changing variable (one predictor), for which I calculated prediction intervals based on the output from the model. In order to calculate prediction intervals around the graphed relationships, I used the function *bootMer* (with arguments *use.u = FALSE* and *type* = "*parametric*") to create 1000 bootstrapped samples of the original data, refitting the model with each bootstrapped sample and recalculating the predicted values for the fake data. The 95% prediction interval for each line in the fake data was calculated as the lower (2.5%) and upper (2.5%) of the distribution of predicted values from the bootstrapped data. For these bootstrap predictions I only estimated variation in the fixed effects (by giving the *re.form=NA* argument to *predict*), because I was only interested in quantifying the uncertainty around the estimated effects of the fixed-effect predictor variables.

3.2.3 Results

Food abundance

In the study period (2014–2017), *Apodemus* mice (55.0%; 66 Yellow-necked Mouse individuals) were the most frequently occurring small mammals in the field, followed by the *Myodes* voles (26.7%; 32 Bank Vole inds), *Microtus* voles (13.3%; 15 Field Vole and one Common Vole inds), and *Sorex* shrews (5.0%, four Common Shrew and two European Pygmy Shrew inds). The abundance of *Apodemus* mice varied substantially between years, showing an increase in 2015 and a peak in 2017 (Fig. 12).

Dietary structure

In the study period (2014–2017), the Boreal Owl males brought to SNBoxes most frequently *Apodemus* mice (2397 inds, 43.6%), followed by *Microtus* voles (1207 inds, 22.0%), *Sorex* shrews (736 inds, 13.4%), birds (633 inds, 11.5%), *Myodes* voles (388 inds, 7.1%), and other prey (130 inds, 2.4%) – Table 2. I also found that 71.0% (1703 inds) of *Apodemus* mice, 65.5% (791 inds) of *Microtus* voles, 96.5% (710 inds) of *Sorex* shrews, 76.5% (297 inds) of *Myodes* voles, and 62.2% (394 inds) of birds were delivered as whole prey (Table 2, Fig. 5). With birds, 29.1% of prey (184 inds) consisted of bird nestlings and 64.1% (406 inds) were adults (for details, see Table 2). In terms of food supply, *Apodemus* mice were taken proportionately with the respect to their abundance in the field, while Bank Voles were not preferred as prey by the owls – for details, see Fig. 12, 13.

Based on weighing the prey items stored in owls' nests, *Apodemus* mice (mean ± SD, 22.4 ± 7.2 g, *n* = 200 inds prey) and *Microtus* voles (22.3 ± 8.1 g, 90 inds) consisted the heaviest stored prey, followed by birds (20.4 ± 17.1 g, *n* = 109 inds prey) and *Myodes* voles (19.4 ± 5.4 g, 74 inds prey). *Sorex* shrews (5.9 ± 2.8 g, *n* = 54 inds prey) were the lightest stored prey.

Figure 12. Population dynamics of *Apodemus* mice, *Microtus* voles, *Myodes* voles, and *Sorex* shrews in the field in 2014–2017 in the study area of the Ore Mts., Czechia. Box: 25–75%; whiskers: non-outlier range; point: median.

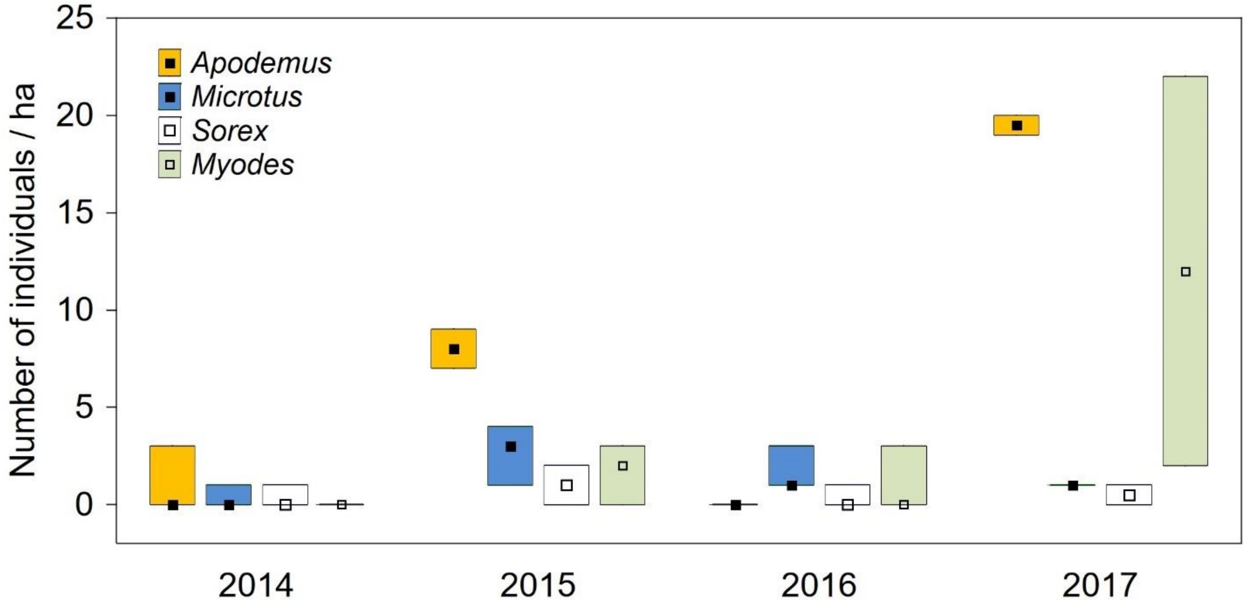


Figure 13. Proportions of prey items by groups — *Apodemus* mice, *Microtus* voles, *Myodes* voles, *Sorex* shrews, and birds — comprising the Boreal Owl diet in 2014–2017 in the study area of the Ore Mts., Czechia. Box: 25–75%; whiskers: non-outlier range; point: median. The nests (n = 41) and prey (n = 5361 prey items) provided by male owls were recorded using SNBoxes. Proportions were calculated separately for each nest, and these values used to create the boxplots.

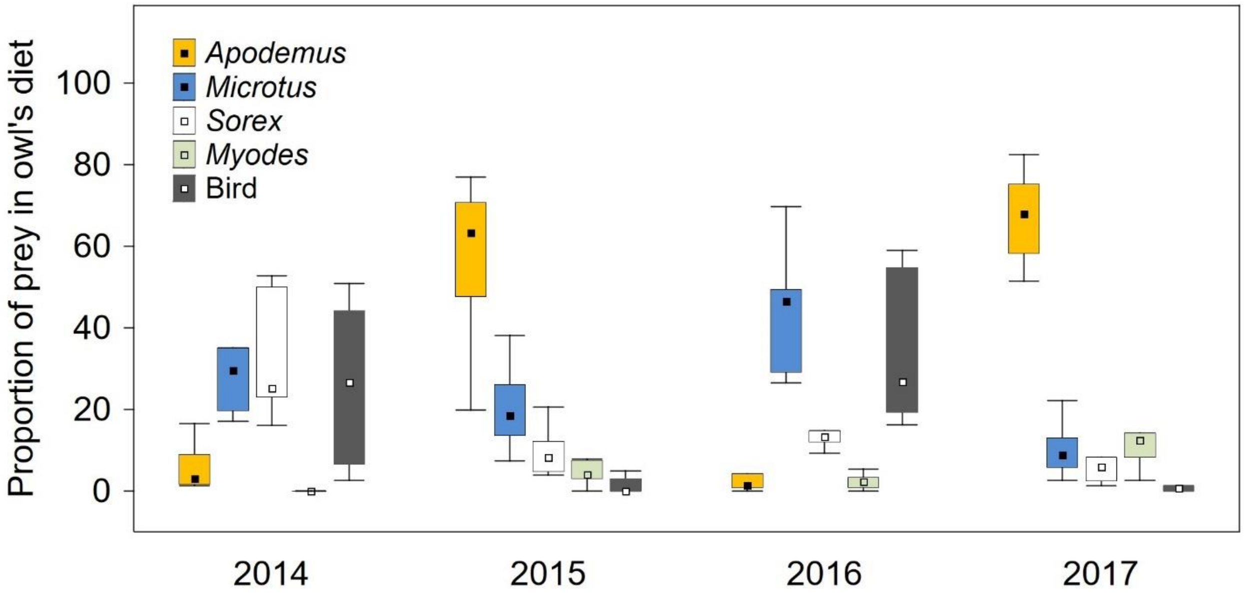


Table 2. The manner with which separate prey groups — *Apodemus* mice, *Microtus* voles, *Myodes* voles, *Sorex* shrews, birds, and other prey — were handled and delivered by the Boreal Owl males to their nestlings in the Ore Mts., Czechia, in 2014–2017 (5491 prey items, 41 nests). The prey was identified as 'complete' (whole prey), 'decapitated', 'only head', 'remains of prey', and "nestling" or "adult" (only for birds), and sorted by numbers and proportions. The prey provided by male owls for their nestlings were recorded using SNBoxes.

Prey group	Prey specification	Handled prey delivered to the nest	Number	%
Apodemus			**2397**	**43.7**
		Complete	*1703*	*71.0*
		Decapitated	*506*	*21.1*
		Only head	*120*	*5.0*
		Remains or prey	*52*	*2.2*
		Unidentified	*16*	*0.7*
Microtus			**1207**	**22.0**
		Complete	*791*	*65.5*
		Decapitated	*296*	*24.5*
		Only head	*30*	*2.5*
		Remains or prey	*84*	*7.0*
		Unidentified	*6*	*0.5*
Myodes			**388**	**7.1**
		Complete	*297*	*76.5*
		Decapitated	*79*	*20.4*
		Only head	*4*	*1.0*
		Remains or prey	*6*	*1.5*
		Unidentified	*2*	*0.5*
Sorex			**736**	**13.4**
		Complete	*710*	*96.5*
		Decapitated	*26*	*3.5*
Birds			**633**	**11.5**
		Complete	*394*	*62.2*
		Decapitated	*123*	*19.4*
		Only head	*40*	*6.3*
		Remains or prey	*67*	*10.6*
		Unidentified	*9*	*1.4*
	Bird nestlings		184	29.1
		Bare nestling	*80*	*43.5*
		Plumy nestling	*104*	*56.5*
	Bird adults		406	64.1
		Feathered adults	*379*	*93.3*
		Plucked adults	*27*	*6.7*
Others			**130**	**2.4**
	Muscardinus avellanarius		**51**	**0.9**
		Complete	*51*	*100.0*
		Decapitated	*0*	*0.0*
	Insect		**1**	**0**
		Complete	*1*	*100.0*
	Mammal unid.		**45**	**0.8**
		Complete	*2*	*4.4*
		Decapitated	*5*	*11.4*
		Only head	*1*	*2.3*
		Remains or prey	*22*	*50.0*
		Unidentified	*15*	*34.1*
Unidentified			**33**	**0.6**
Total			**5491**	**100**

Predictors of provisioning rate

The Boreal Owl males increased their prey delivery rate with increasing numbers and age of nestlings (Fig. 14 and 15, Table 3). With respect to the small male hypothesis, I found that lighter males provided significantly more prey items than heavier males, but only at nests with smaller and intermediate numbers of nestlings (Table 3). This statistical interaction between male body mass and brood size was statistically significant (Table 3). As can be seen from Fig. 15, the differences in the body mass of the male owls were the largest when the males provided for one or two nestlings, becoming smaller with increasing brood size, which was then followed by a decreasing disproportionality in the provisioning rate between lighter and heavier males. The effect of male body mass on the provisioning rate completely disappeared when the males provided for six or seven nestlings, and reversed for the largest broods, with heavier males provided more prey items for their nestlings than lighter males (Fig. 15). Finally, I found that neither the wing length, calendar day, nor the abundance of either *Apodemus* or *Microtus* affected the provisioning rate of the Boreal Owl males.

Table 3. Results from the analysis in which the prey delivery rate by Boreal Owl males (the number or prey items delivered to the nestlings per night) were modelled in relation to the listed predictors and their interactions. A negative binomial mixed model fitted using restricted maximum likelihood was fitted to the data.

Prey delivery rate	Estimate	Std. Error	Upper 95% conf. limit	Lower 95% conf. limit	Z value	Pr(>|z|)
(Intercept)	**1.3750**	**0.1492**	**1.6734**	**1.0766**	**9.2160**	**< 2e-16**
Body mass	**-0.0488**	**0.0118**	**-0.0253**	**-0.0723**	**-4.1460**	**0.0000**
Wing length	-0.0049	0.0106	0.0163	-0.0261	-0.4610	0.6448
Brood size	**0.1046**	**0.0143**	**0.1332**	**0.0760**	**7.3280**	**0.0000**
Nestling age	**0.0039**	**0.0019**	**0.0078**	**0.0000**	**2.0080**	**0.0446**
Calendar day	-0.0008	0.0008	0.0008	-0.0024	-0.9630	0.3356
Apodemus abundance	0.0038	0.0044	0.0125	-0.0050	0.8570	0.3913
Microtus abundance	0.0124	0.0299	0.0722	-0.0473	0.4160	0.6775
Wing length*Body mass	-0.0006	0.0008	0.0010	-0.0022	-0.7230	0.4699
Wing length*Brood size	-0.0001	0.0028	0.0056	-0.0058	-0.0330	0.9735
Body mass*Brood size	**0.0071**	**0.0024**	**0.0119**	**0.0024**	**2.9870**	**0.0028**

Figure 14. The probability of prey delivery rate by the Boreal Owl males in relation to nestlings' age (the oldest nestling). The expected number of prey items delivered to nests by the male owls and its upper (97.5%) and lower (2.5%) prediction intervals are shown.

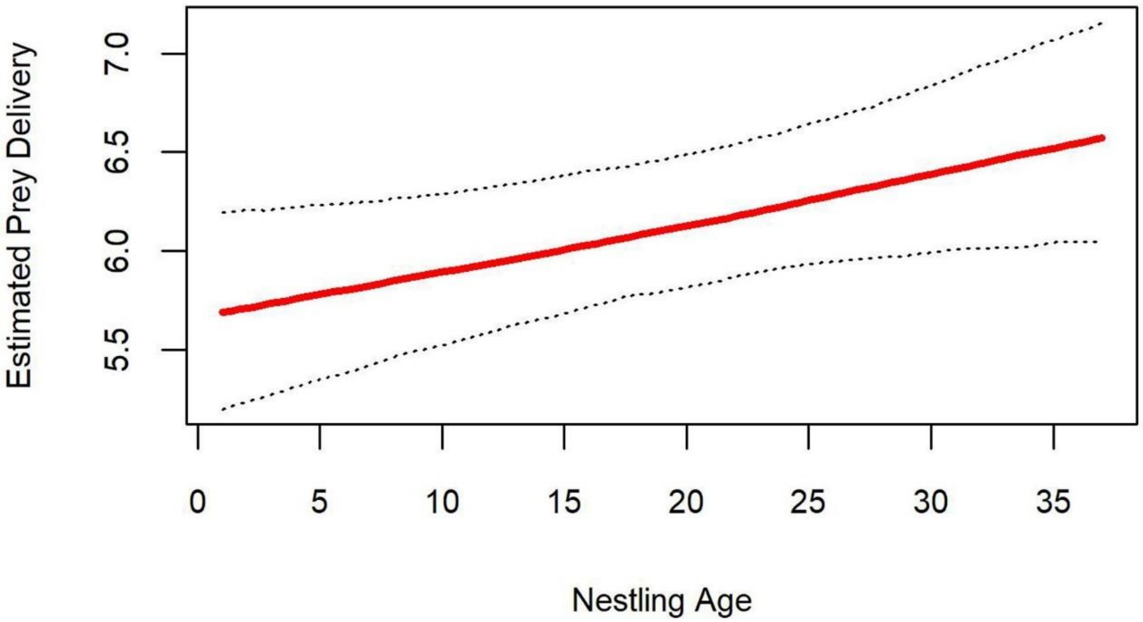
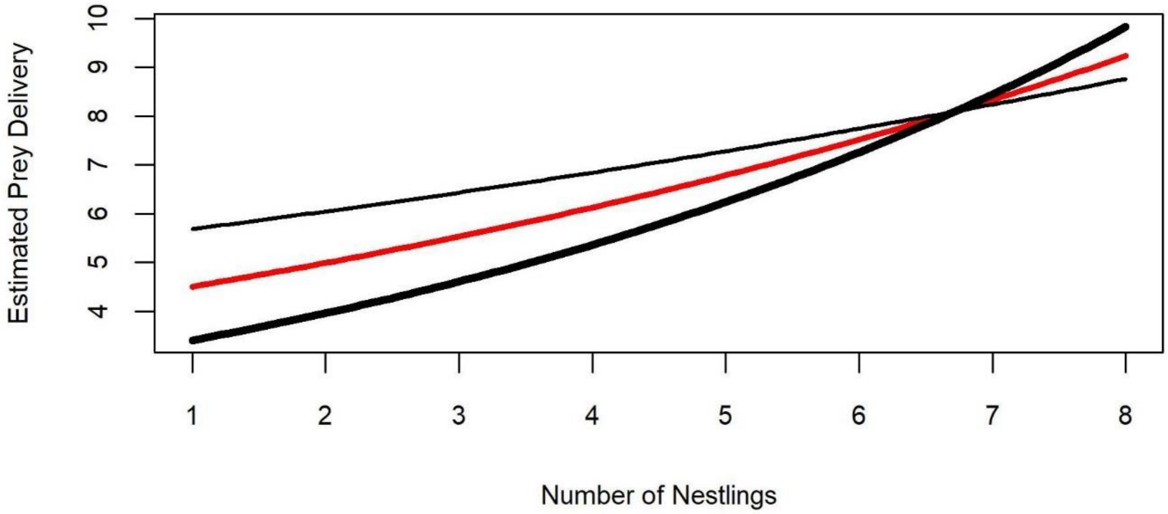


Figure 15. Male Boreal Owl probability of prey delivery rate varies as an interaction between brood size (the number of nestlings provisioned) and body mass. Thinner black, red, and thicker black lines represent the expected probability of prey delivery rate for males with the 10th quantile, median, and 90th quantile, respectively, of the male body mass.



Predictors of the proportion of the provided prey type

Apodemus prey

The proportion of *Apodemus* mice in the Boreal Owl’s diet was not affected either by body mass or wing length of the males (Table 4). Additionally, I found that the proportion of *Apodemus* mice in the owl’s diet significantly increased with the number (Fig. 16) and age (Fig. 17) of the nestlings being provisioned (Table 4); broods of seven or eight nestlings could expect to receive an *Apodemus* mouse prey with up to a 50–70% probability (the upper prediction interval, Fig. 16), and the nestlings at the time of fledgling with additional a 30–40% probability (Fig. 17). In relation to environmental conditions, the probability of *Apodemus* mice delivery increased with the increasing abundance of both *Apodemus* mice (Fig. 18) and *Microtus* voles (Fig. 19), and decreased with progression of the breeding season (i.e., calendar day, Fig. 20). Other predictors had no effects on the proportion of *Apodemus* mice delivered to nests (Table 4).

Table 4. Results from the analysis in which the proportion of *Apodemus* prey delivered by the Boreal Owl males to their nestlings were modelled in relation to the listed predictors and their interactions. A binomial mixed model fitted using restricted maximum likelihood was fitted to the data.

Apodemus prey	Estimate	Std. Error	Upper 95% conf. limit	Lower 95% conf. limit	Z value	Pr(>|z|)
(Intercept)	**-4.9130**	**1.1205**	**-2.6720**	**-7.1541**	**-4.3850**	**0.0000**
Body mass	-0.0249	0.0838	0.1426	-0.1925	-0.2980	0.7660
Wing length	0.0428	0.0817	0.2061	-0.1206	0.5240	0.6006
Brood size	**0.3113**	**0.0897**	**0.4906**	**0.1319**	**3.4700**	**0.0005**
Nestling age	**0.0301**	**0.0150**	**0.0601**	**0.0002**	**2.0140**	**0.0441**
Calendar day	**-0.0174**	**0.0051**	**-0.0073**	**-0.0275**	**-3.4350**	**0.0006**
Prey delivery rate	0.0227	0.0401	0.1029	-0.0574	0.5670	0.5708
***Apodemus* abundance**	**0.2334**	**0.0360**	**0.3053**	**0.1614**	**6.4870**	**0.0000**
***Microtus* abundance**	**1.4911**	**0.2856**	**2.0624**	**0.9199**	**5.2200**	**0.0000**
Wing length*Body mass	0.0058	0.0043	0.0145	-0.0028	1.3490	0.1773
Wing length*Brood size	-0.0115	0.0180	0.0244	-0.0474	-0.6400	0.5221
Body mass*Brood size	0.0165	0.0170	0.0505	-0.0176	0.9680	0.3332

Figure 16. The probability of *Apodemus* prey delivery to nests by the Boreal Owl males in relation to brood size (the number of nestlings provisioned). The expected probability of *Apodemus* delivery and their upper (97.5%) and lower (2.5%) prediction intervals are shown.

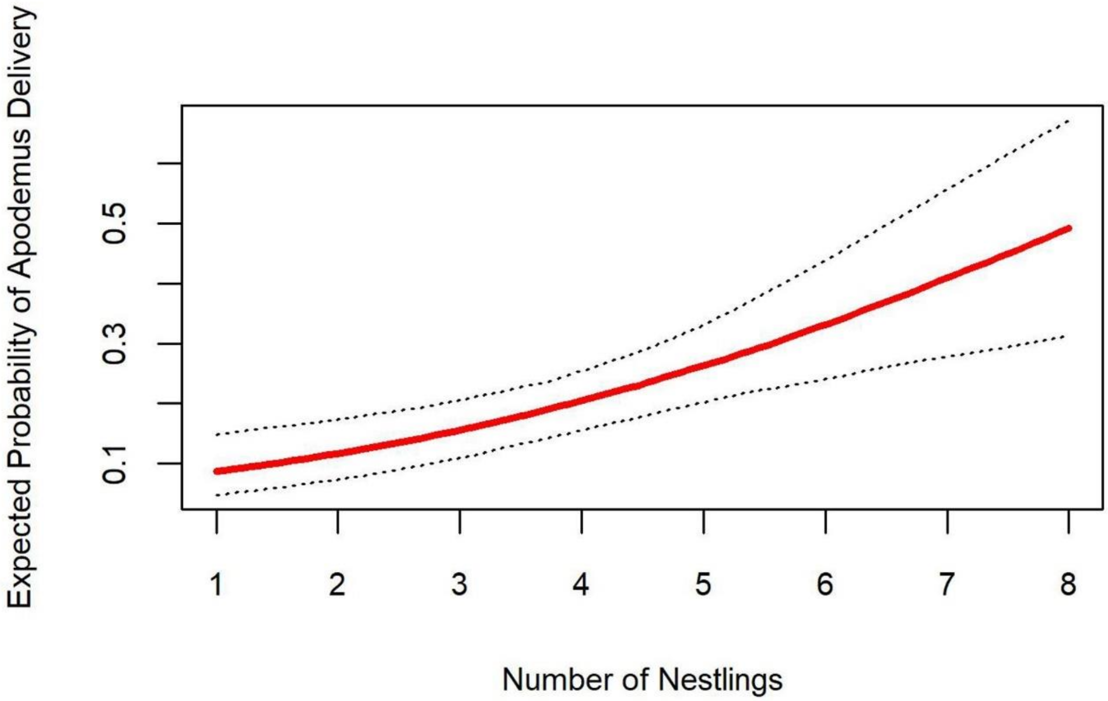


Figure 17. The probability of *Apodemus* prey delivery to nests by the Boreal Owl males in relation to nestlings' ages (the oldest nestling). The expected probability of *Apodemus* delivery and its upper (97.5%) and lower (2.5%) prediction intervals are shown.

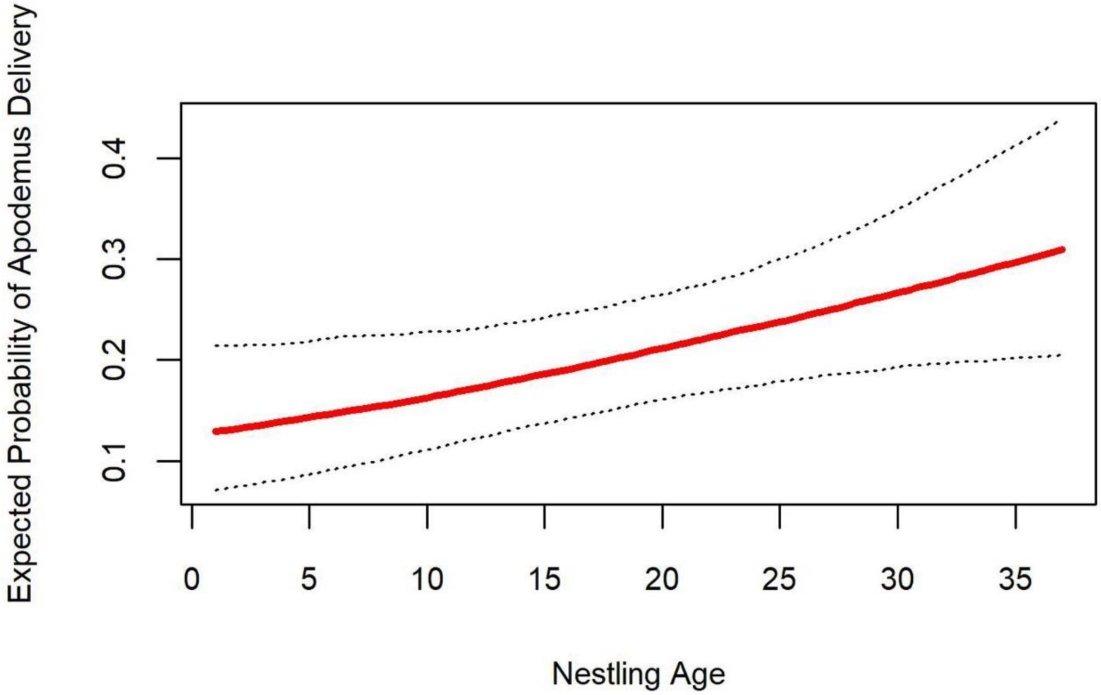


Figure 18. The probability of *Apodemus* prey delivery to nests by the Boreal Owl males in relation to the abundance of *Apodemus* mice in the field. The expected probability of *Apodemus* delivery and its upper (97.5%) and lower (2.5%) prediction intervals are shown.

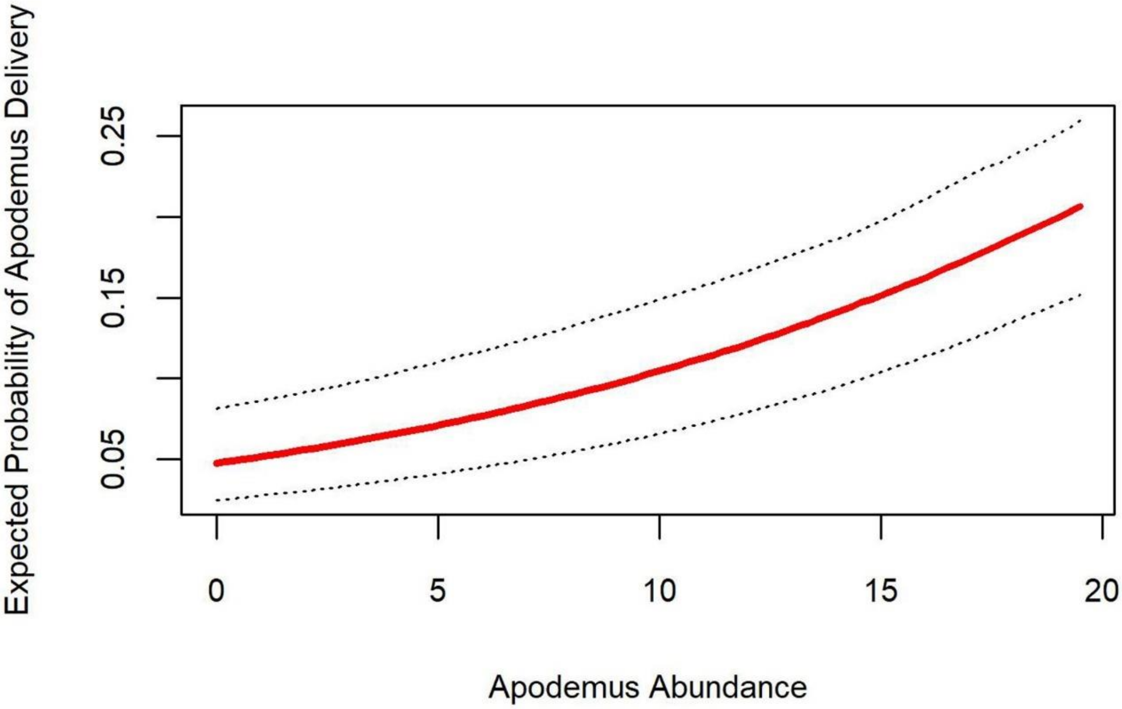


Figure 19. The probability of *Apodemus* prey delivery to nests by the Boreal Owl males in relation to the abundance of *Microtus* voles in the field. The expected probability of *Apodemus* delivery and its upper (97.5%) and lower (2.5%) prediction intervals are shown.

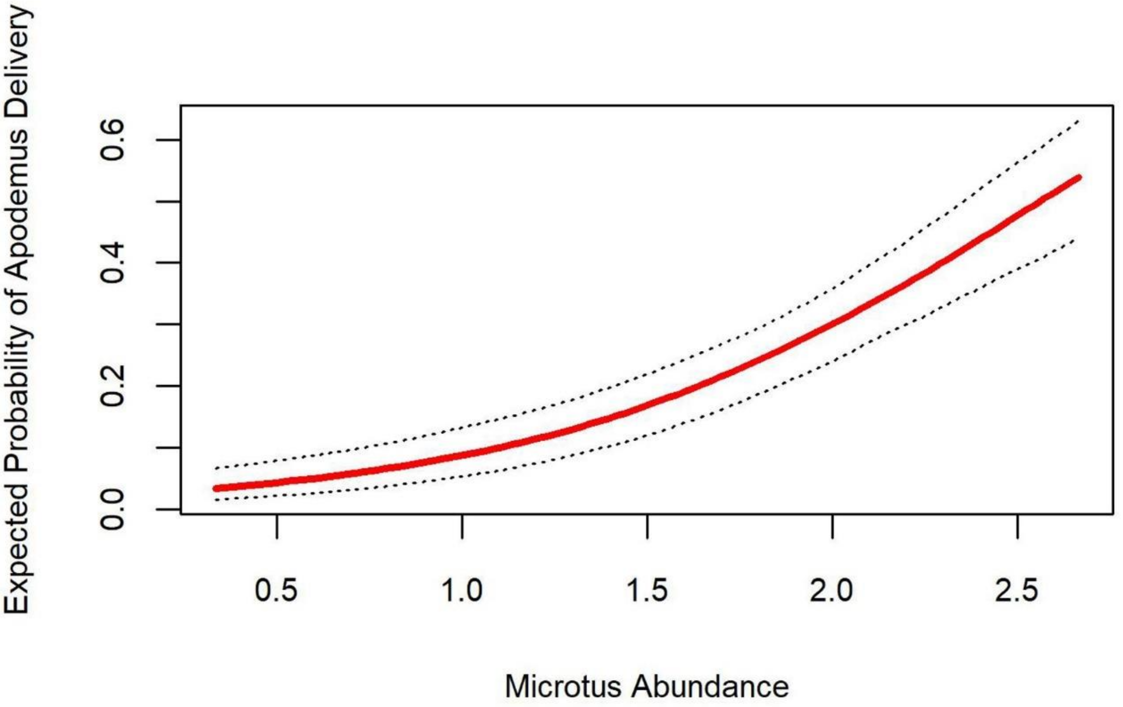
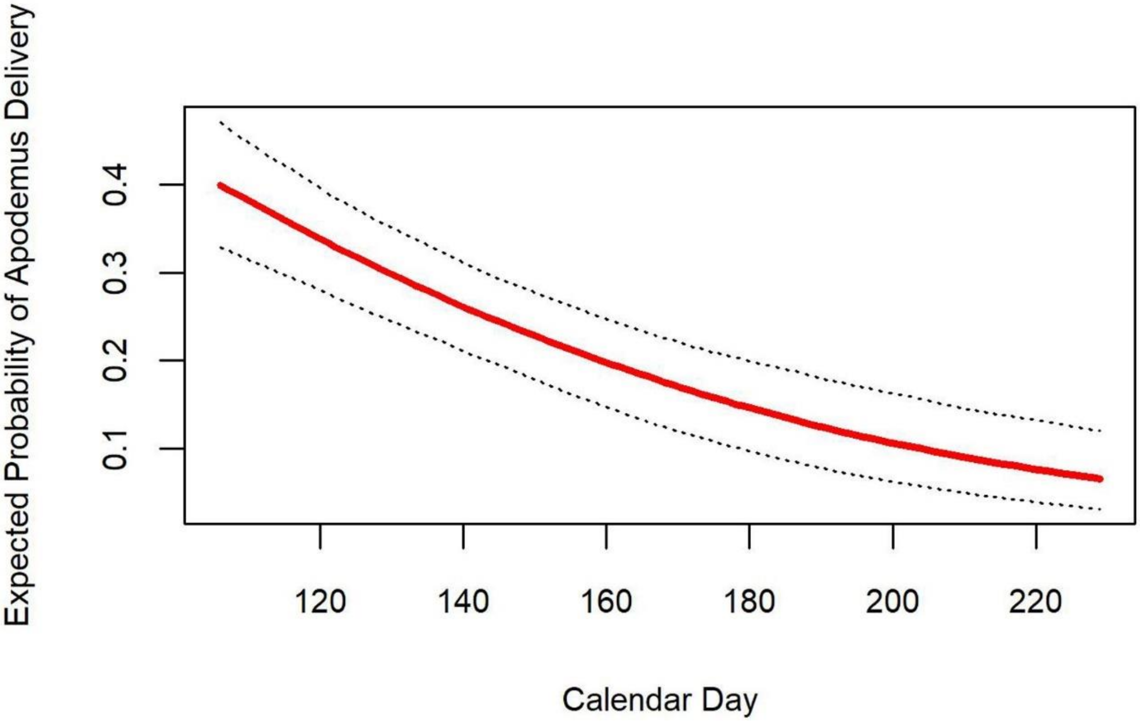


Figure 20. The probability of *Apodemus* prey delivery to nests by the Boreal Owl males in relation to calendar day (since 1 January). The expected probability of *Apodemus* delivery and its upper (97.5%) and lower (2.5%) prediction intervals are shown.



Microtus prey

The proportion of *Microtus* voles in the Boreal Owl’s diet was not affected either by body mass or wing length of the males (Table 5), but it increased with decreasing prey delivery rate (Fig. 21, Table 5). Additionally, the proportion of *Microtus* voles in the owls’ diet significantly increased with decreasing abundance of *Apodemus* mice in the field (Fig. 22), but was not related with the abundance of *Microtus* voles (Table 5). Other predictors had no effects on the proportion of *Microtus* prey delivery (Table 5).

Table 5. Results from the analysis in which the proportion of *Microtus* prey delivered by the Boreal Owl males to their nestlings were modelled in relation to the listed predictors and their interactions. A binomial mixed model fitted using restricted maximum likelihood was fitted to the data.

Microtus prey	Estimate	Std. Error	Upper 95% conf. limit	Lower 95% conf. limit	Z value	Pr(>|z|)
(Intercept)	-1.3808	0.8210	0.2612	-3.0227	-1.6820	0.0926
Body mass	0.0799	0.0563	0.1925	-0.0328	1.4180	0.1563
Wing length	-0.0026	0.0436	0.0846	-0.0898	-0.0590	0.9526
Brood size	0.0226	0.0974	0.2173	-0.1721	0.2320	0.8168
Nestling age	0.0001	0.0127	0.0255	-0.0253	0.0090	0.9928
Calendar day	0.0051	0.0047	0.0145	-0.0042	1.0960	0.2729
Prey delivery rate	**-0.1168**	**0.0469**	**-0.0230**	**-0.2107**	**-2.4910**	**0.0127**
***Apodemus* abundance**	**-0.1984**	**0.0374**	**-0.1237**	**-0.2732**	**-5.3110**	**0.0000**
Microtus abundance	0.2451	0.1633	0.5716	-0.0815	1.5010	0.1333
Wing length*Body mass	-0.0022	0.0043	0.0065	-0.0108	-0.5070	0.6119
Wing length*Brood size	0.0082	0.0135	0.0352	-0.0189	0.6050	0.5452
Body mass*Brood size	-0.0197	0.0163	0.0130	-0.0523	-1.2050	0.2283

Figure 21. The probability of *Microtus* prey delivery to nests by the Boreal Owl males in relation to the prey delivery rate (the number of prey items delivered per night). The expected probability of *Microtus* delivery and its upper (97.5%) and lower (2.5%) prediction intervals are shown.

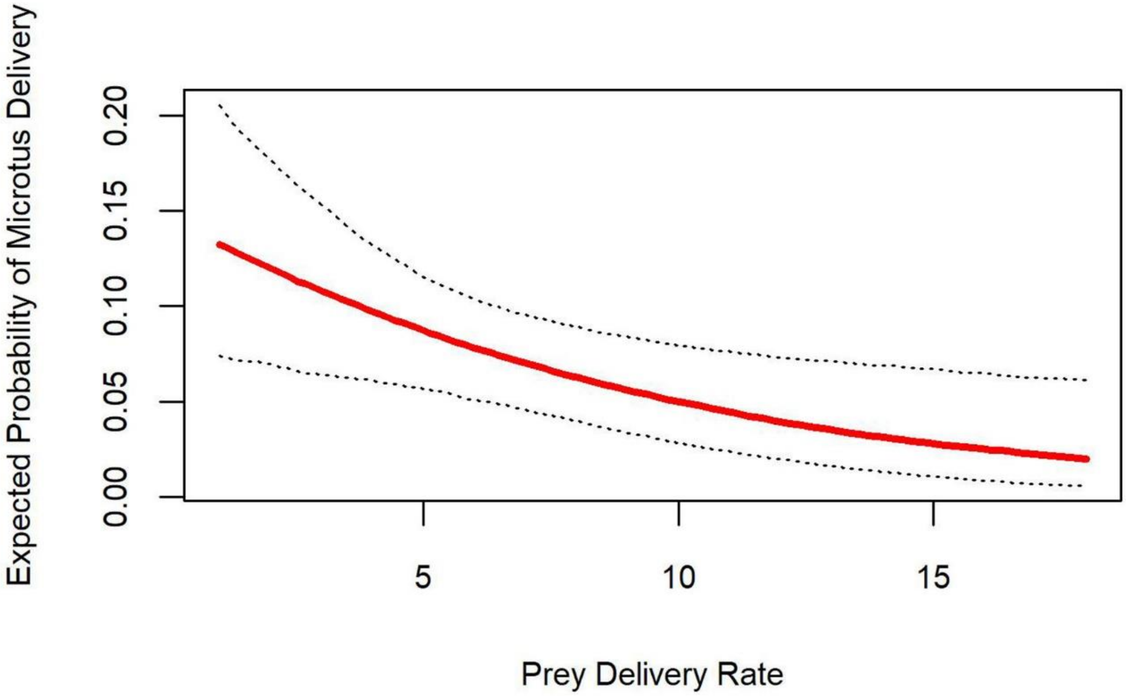
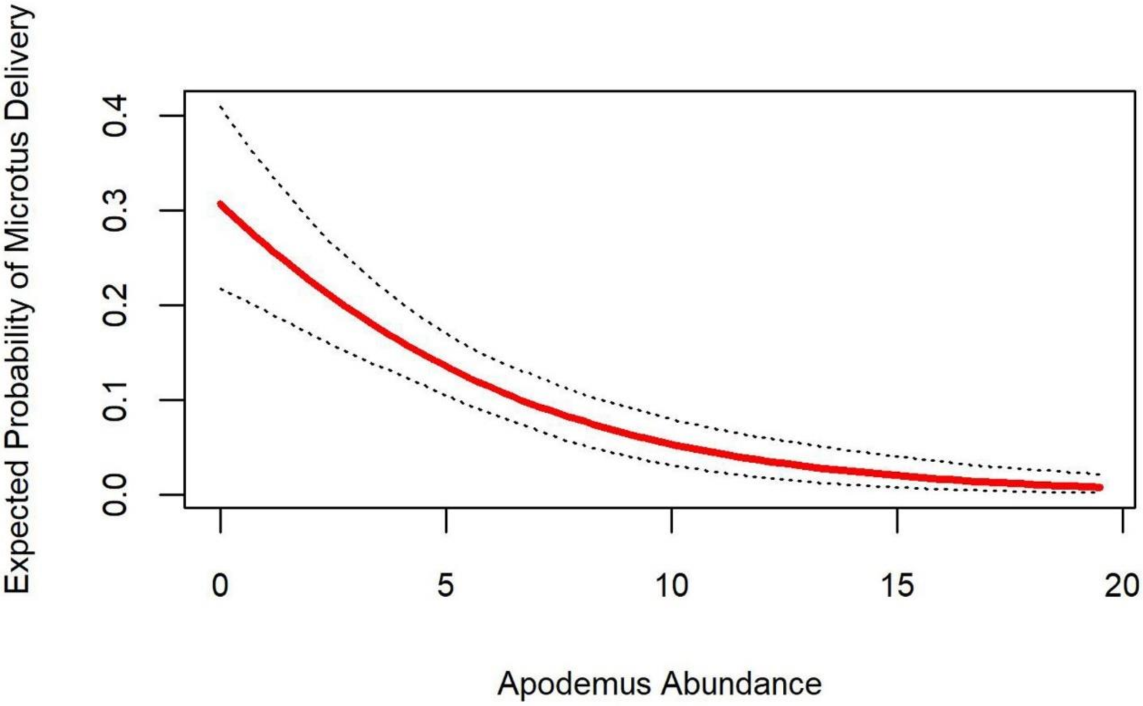


Figure 22. The probability of *Microtus* prey delivery to nests by the Boreal Owl males in relation to the abundance of *Apodemus* mice in the field. The expected probability of *Microtus* delivery and its upper (97.5%) and lower (2.5%) prediction intervals are shown.



Sorex prey

The proportion of *Sorex* shrews in the Boreal Owl's diet was influenced neither body mass nor by wing length of the males (Table 6). At the same time, the proportion of *Sorex* shrews in the owl's diet significantly increased with decreasing abundance of both *Apodemus* mice (Fig. 23) and *Microtus* voles (Fig. 24) and with increasing prey delivery rate (Fig. 25, Table 6). Other predictors had no effects on the proportion of *Sorex* prey delivery (Table 6).

Table 6. Results from the analysis in which the proportion of *Sorex* prey delivered by the Boreal Owl males to their nestlings were modelled in relation to the listed predictors and their interactions. A binomial mixed model fitted using restricted maximum likelihood was fitted to the data.

Sorex prey	Estimate	Std. Error	Upper 95% conf. limit	Lower 95% conf. limit	Z value	Pr(>|z|)
(Intercept)	-0.2673	1.2209	2.1746	-2.7091	-0.2190	0.8267
Body mass	0.1218	0.0813	0.2844	-0.0407	1.4990	0.1339
Wing length	-0.0327	0.0703	0.1079	-0.1734	-0.4660	0.6415
Brood size	0.0621	0.1514	0.3650	-0.2408	0.4100	0.6818
Nestling age	0.0091	0.0175	0.0440	-0.0259	0.5190	0.6041
Calendar day	-0.0085	0.0071	0.0058	-0.0228	-1.1860	0.2356
Prey delivery rate	**0.1233**	**0.0568**	**0.2369**	**0.0098**	**2.1720**	**0.0299**
***Apodemus* abundance**	**-0.1453**	**0.0428**	**-0.0598**	**-0.2309**	**-3.3980**	**0.0007**
***Microtus* abundance**	**-1.0887**	**0.2366**	**-0.6154**	**-1.5620**	**-4.6010**	**0.0000**
Wing length*Body mass	0.0023	0.0059	0.0142	-0.0095	0.3960	0.6923
Wing length*Brood size	0.0142	0.0253	0.0648	-0.0364	0.5610	0.5750
Body mass*Brood size	-0.0203	0.0216	0.0229	-0.0635	-0.9390	0.3480

Figure 23. The probability of *Sorex* prey delivery to nests by the Boreal Owl males in relation to the abundance of *Apodemus* mice in the field. The expected probability of *Sorex* prey delivery and its upper (97.5%) and lower (2.5%) prediction intervals are shown.

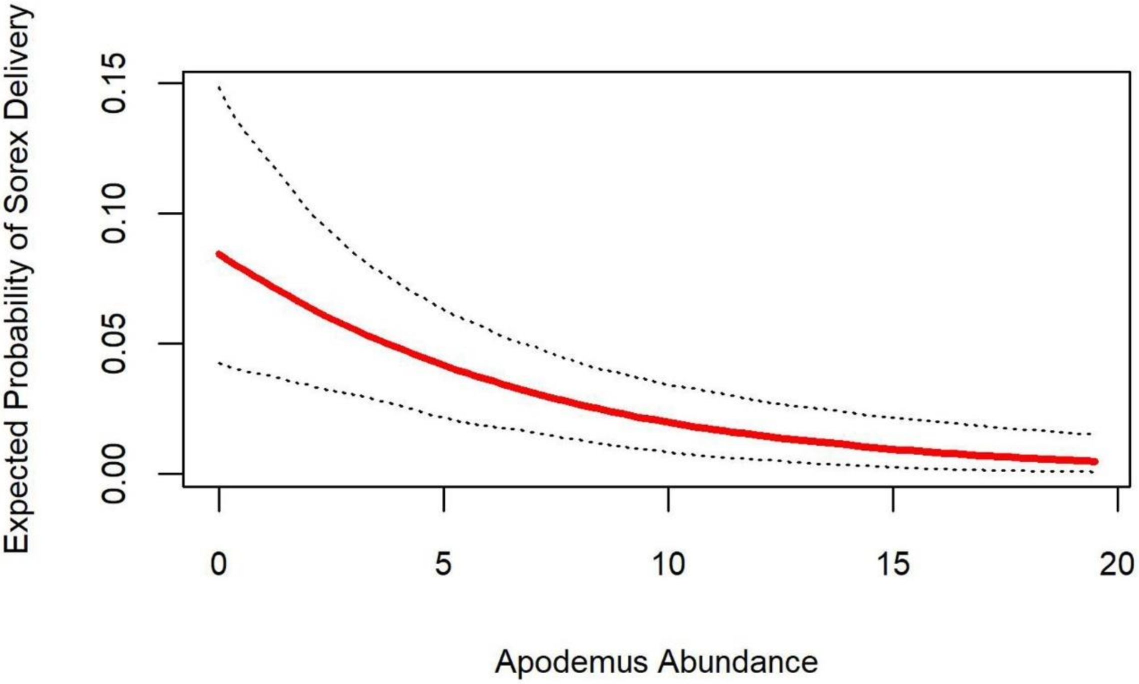


Figure 24. The probability of *Sorex* prey delivery to nests by the Boreal Owl males in relation to the abundance of *Microtus* voles in the field. The expected probability of *Sorex* prey delivery and its upper (97.5%) and lower (2.5%) prediction intervals are shown.

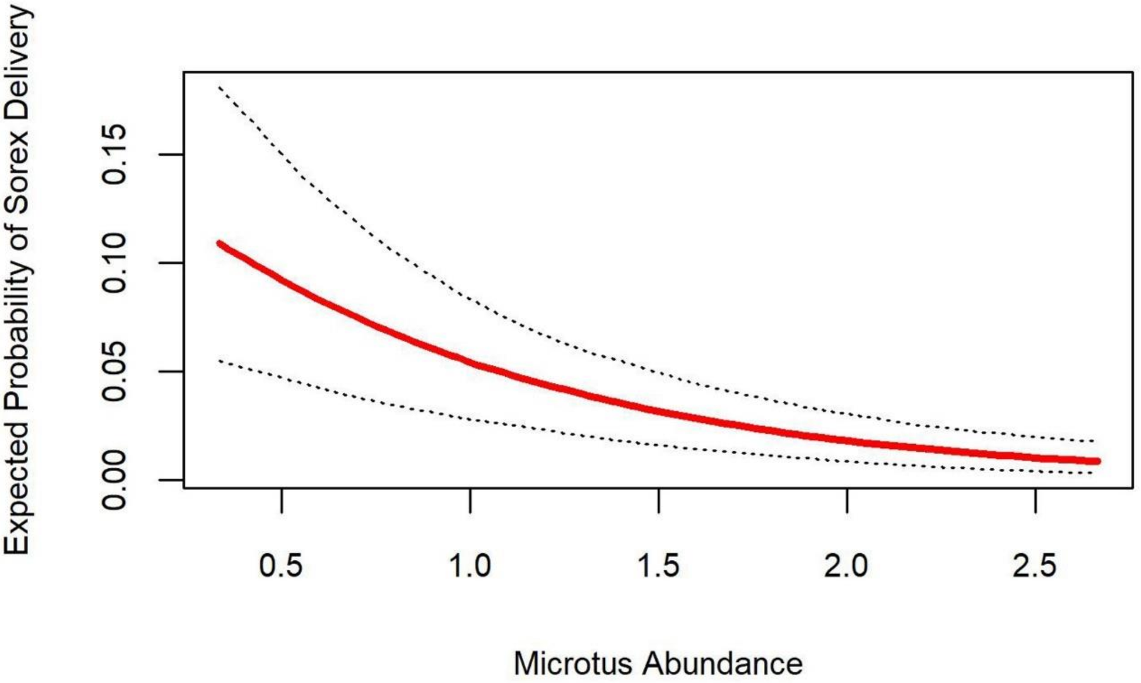
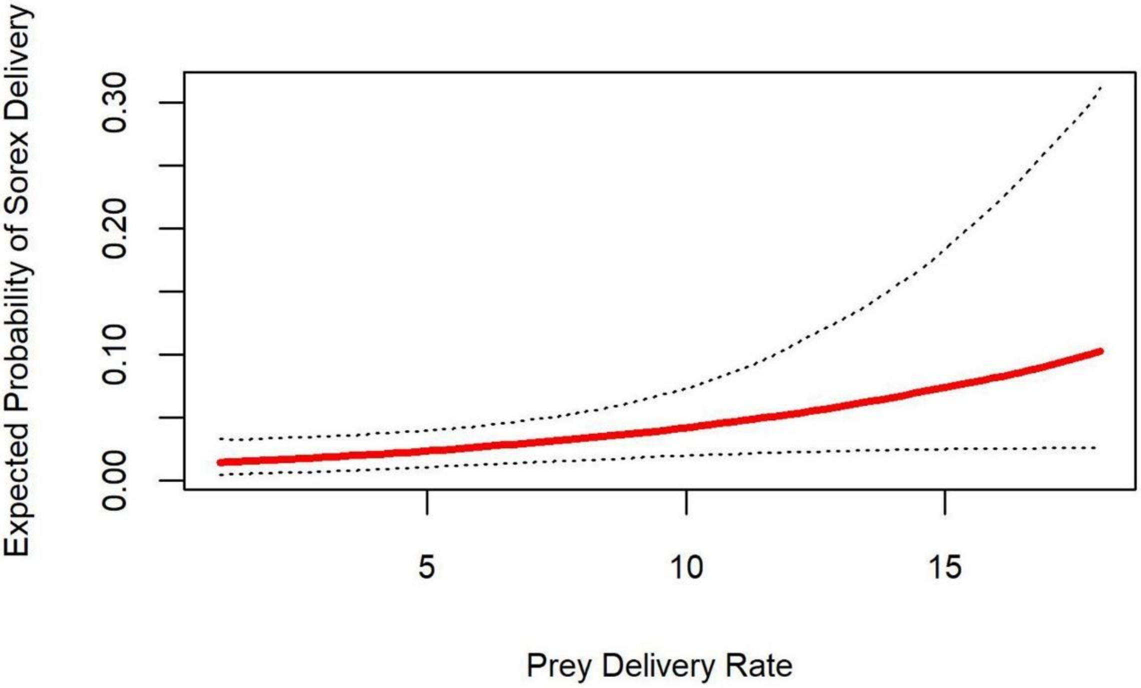


Figure 25. The probability of *Sorex* prey delivery to nests by the Boreal Owl males in relation to the prey delivery rate. The expected probability of *Sorex* prey delivery and its upper (97.5%) and lower (2.5%) prediction intervals are shown.



Myodes prey

None of the predictors had an effect on the proportion of Bank Voles in the Boreal Owl's diet (Table 7).

Table 7. Results from the analysis in which the proportion of Bank Vole (*Myodes glareolus*) prey delivered by the Boreal Owl males to their nestlings were modelled in relation to the listed predictors and their interactions. A binomial mixed model fitted using restricted maximum likelihood was fitted to the data.

Myodes vole	Estimate	Std. Error	Upper 95% conf. limit	Lower 95% conf. limit	Z value	Pr(>|z|)
(Intercept)	-7.5985	6.3311	5.0637	-20.2606	-1.2000	0.2301
Body mass	-0.3176	0.2269	0.1362	-0.7714	-1.4000	0.1616
Wing length	0.0900	0.3512	0.7923	-0.6123	0.2560	0.7978
Brood size	0.1112	0.2060	0.5233	-0.3009	0.5400	0.5894
Nestling age	-0.0895	0.0459	0.0023	-0.1813	-1.9490	0.0513
Calendar day	-0.0174	0.0115	0.0057	-0.0404	-1.5070	0.1318
Prey delivery rate	-0.1524	0.1134	0.0743	-0.3792	-1.3450	0.1788
Apodemus supply	0.4247	0.2413	0.9072	-0.0578	1.7600	0.0783
Microtus supply	1.3175	1.3809	4.0793	-1.4443	0.9540	0.3400
Wing length*Body mass	0.0276	0.0332	0.0940	-0.0389	0.8300	0.4065
Wing length*Brood size	-0.0184	0.0732	0.1281	-0.1649	-0.2510	0.8017
Body mass*Brood size	0.0313	0.0426	0.1165	-0.0540	0.7340	0.4631

Bird prey

First, I found a relationship between the proportion of bird prey provided by the Boreal Owl males and the interaction between body mass and wing length (Table 8). As we can see from Fig. 26, males with shorten wings provided bird prey with a higher probability than those with longer wings, although this effect only worked for lighter than median-weight males, and the most evident effect was found for the lightest males who delivered bird prey with up to 40% probability. Second, the probability of bird prey occurrence in the owl's diet increased with decreasing brood size, and the significant interaction between the number of nestlings provisioned and wing length has been revealed. The males with shorten wings who provided for from three to eight nestlings delivered bird prey more frequently than those males with longer wings, although the probability of bird delivery by these males only reached about 5% (Fig. 27, Table 8). The effect of wing length on the probability of bird prey delivery disappeared when the males provided for two nestlings, and reversed when they provided for only one nestling: the males with longer wings provisioned their nestling with bird prey more frequently than the males with shorten wings and the probability of bird delivery by these males reached 15%. Third, the probability of bird prey delivery increased when hatchling owls were provisioned, but on average birds only represented up to 3% of delivered items (the upper prediction interval, Fig. 28, Table 8). Finally, the occurrence of bird prey varied with environmental conditions: males provided bird prey more frequently later in the breeding season (Fig. 29) and with increasing abundance of *Microtus* voles in the field (Fig. 30), but they reduced bird prey delivery with increasing abundance of *Apodemus* mice (Fig. 31).

Table 8. Results from the analysis in which the proportion of bird prey delivered by the Boreal Owl males to their nestlings were modelled in relation to the listed predictors and their interactions. A binomial mixed model fitted using restricted maximum likelihood was fitted to the data.

Bird prey	Estimate	Std. Error	Upper 95% conf. limit	Lower 95% conf. limit	Z value	Pr(>|z|)
(Intercept)	**-3.7154**	**1.2183**	**-1.2787**	**-6.1520**	**-3.0500**	**0.0023**
Body mass	0.0139	0.0697	0.1532	-0.1254	0.1990	0.8421
Wing length	**0.1475**	**0.0539**	**0.2554**	**0.0396**	**2.7350**	**0.0062**
Brood size	**-1.0788**	**0.1920**	**-0.6948**	**-1.4627**	**-5.6190**	**0.0000**
Nestling age	**-0.0381**	**0.0148**	**-0.0085**	**-0.0678**	**-2.5730**	**0.0101**
Calendar day	**0.0253**	**0.0069**	**0.0392**	**0.0115**	**3.6520**	**0.0003**
Prey delivery rate	-0.0012	0.0549	0.1086	-0.1111	-0.0220	0.9822
***Apodemus* supply**	**-0.1223**	**0.0482**	**-0.0260**	**-0.2186**	**-2.5390**	**0.0111**
***Microtus* supply**	**0.4624**	**0.2100**	**0.8824**	**0.0424**	**2.2020**	**0.0277**
Wing length*Body mass	**0.0143**	**0.0071**	**0.0285**	**0.0001**	**2.0210**	**0.0433**
Wing length*Brood size	**-0.0845**	**0.0221**	**-0.0403**	**-0.1288**	**-3.8220**	**0.0001**
Body mass*Brood size	-0.0290	0.0267	0.0243	-0.0823	-1.0870	0.2770

Figure 26. Male Boreal Owls probability of delivering bird prey to their nests varies as an interaction between body mass and wing length. Thinner black, red, and thicker black lines represent the expected probabilities of bird prey delivery for males with the 10th quantile, median, and 90th quantile, respectively, of the male wing lengths.

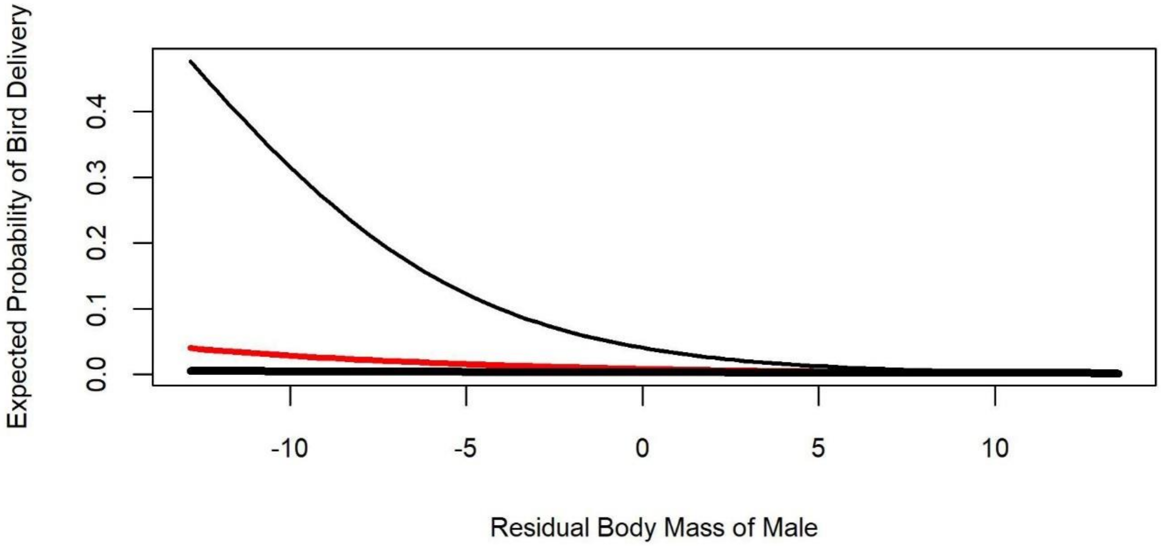


Figure 27. Male Boreal Owls probability of delivering bird prey to their nests varies as an interaction between brood size (the number of nestlings provisioned) and wing length. Thinner black, red, and thicker black lines represent the expected probabilities of bird prey delivery for males with the 10th quantile, median, and 90th quantile, respectively, of the male wing lengths.

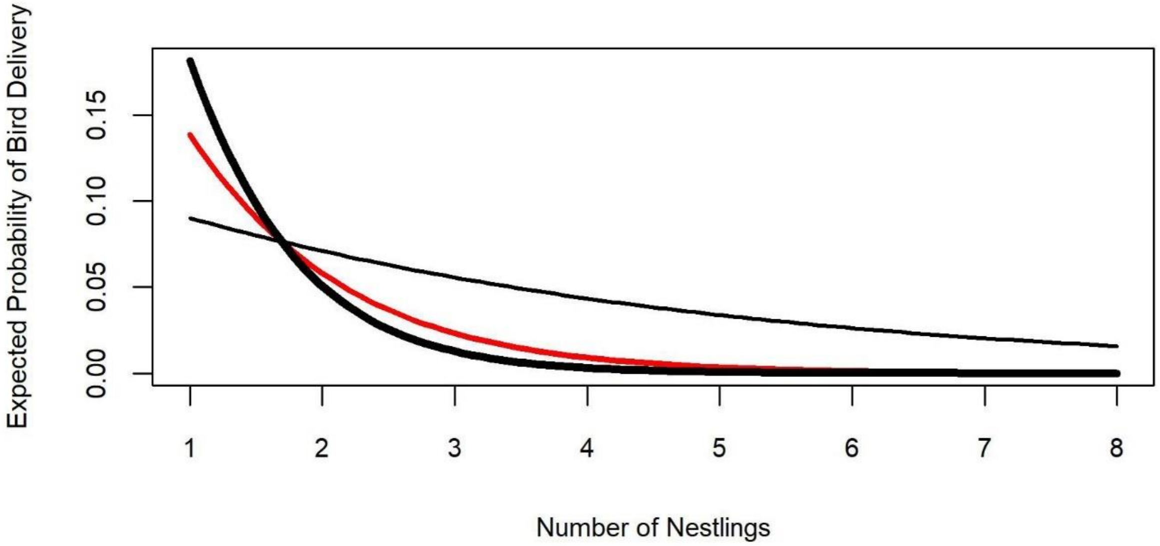


Figure 28. The probability of bird prey delivery to nests by the Boreal Owl males in relation to nestlings' ages (the oldest nestling). The expected probability of bird prey delivery and its upper (97.5%) and lower (2.5%) prediction intervals are shown.

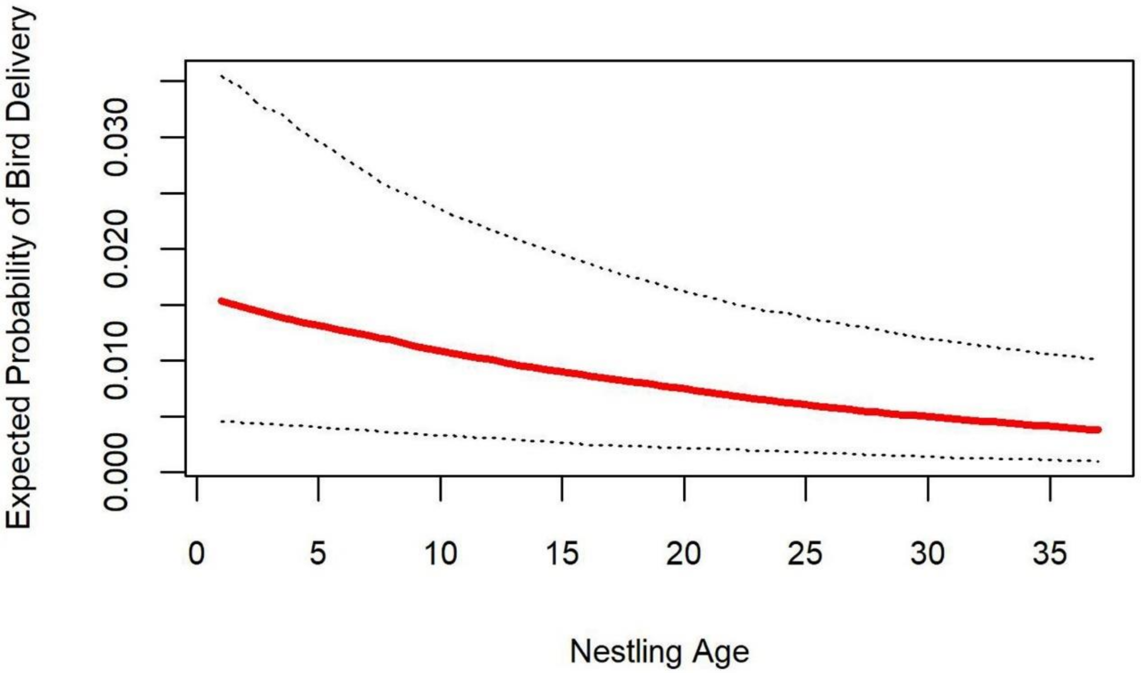


Figure 29. The probability of bird prey delivery to nests by the Boreal Owl males in relation to calendar day (since 1 January). The expected probability of bird prey delivery and its upper (97.5%) and lower (2.5%) prediction intervals are shown.

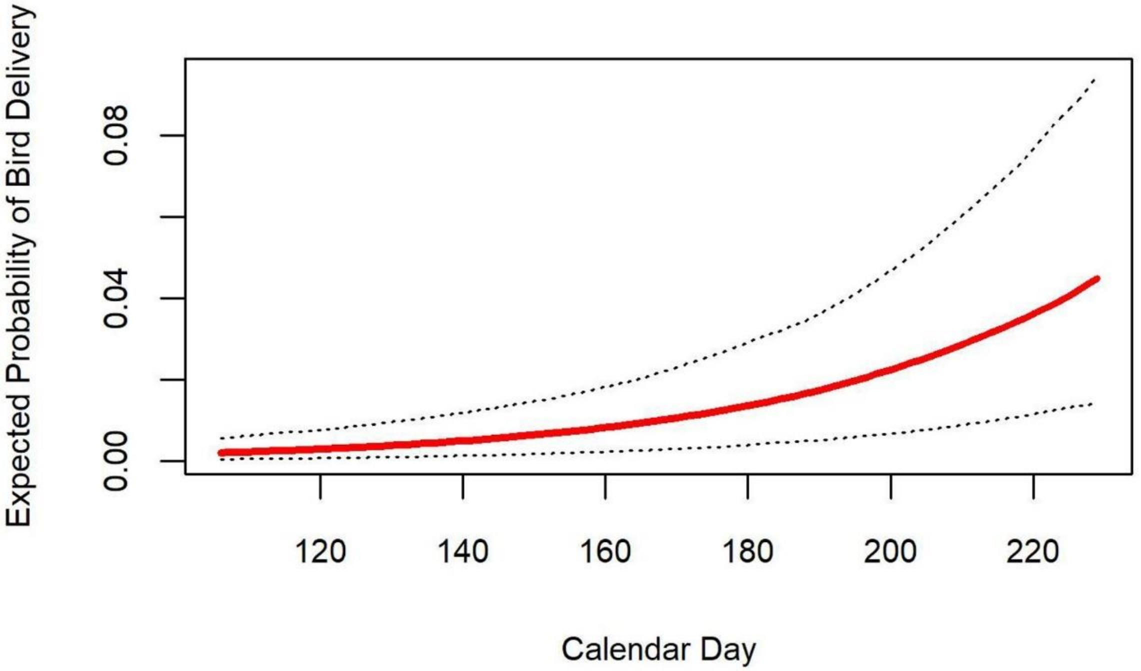


Figure 30. The probability of bird prey delivery to nests by the Boreal Owl males in relation to the abundance of *Microtus* voles in the field. The expected probability of bird prey delivery and the upper (97.5%) and lower (2.5%) prediction intervals are shown.

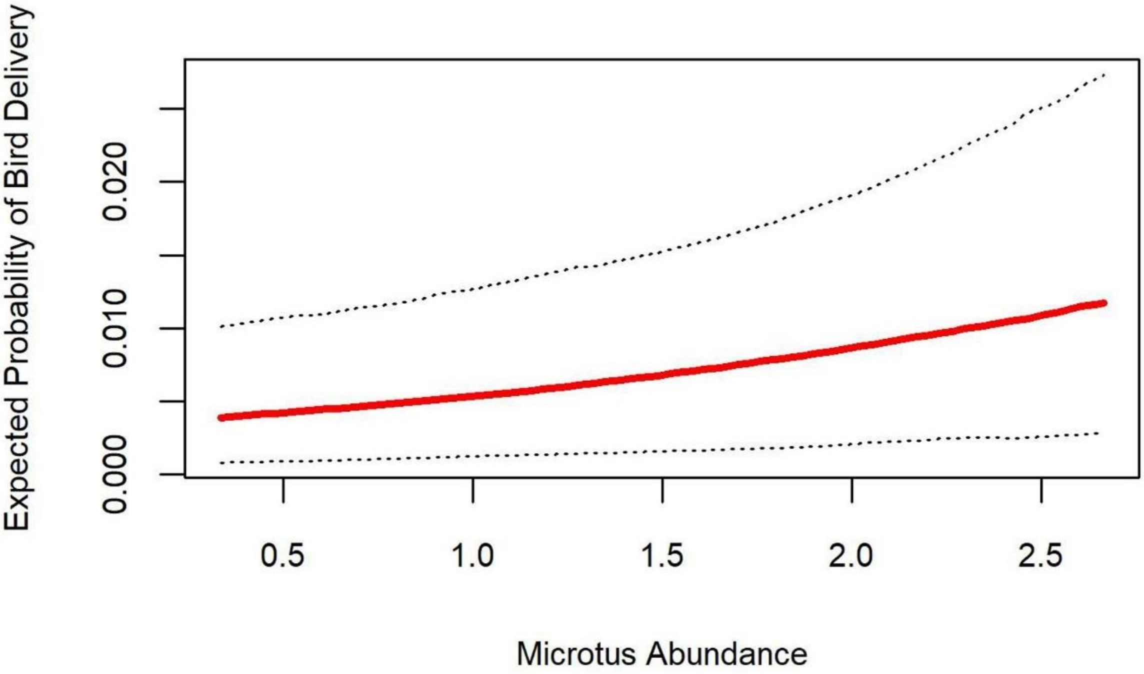
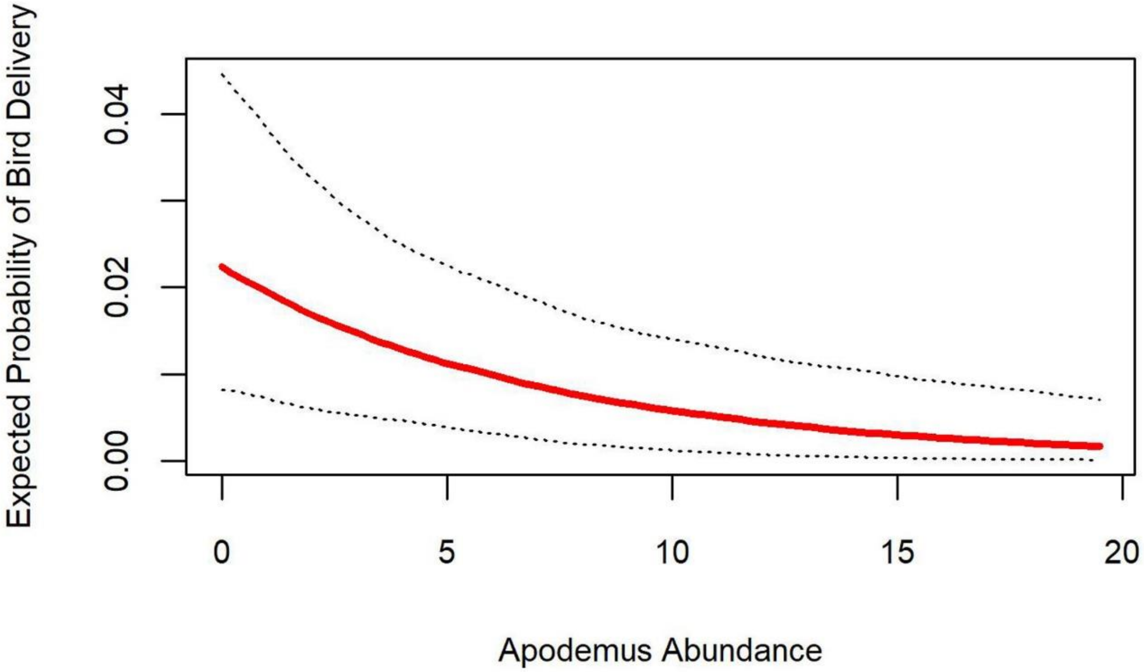


Figure 31. The probability of bird prey delivery to nests by the Boreal Owl males in relation to the abundance of *Apodemus* mice in the field. The expected probability of bird prey delivery and its upper (97.5%) and lower (2.5%) prediction intervals are shown.



3.2.4 Assessing support for the small male hypothesis

Several studies have considered the reason for the evolution of reversed size sexual dimorphism in birds of prey, and one of the most widely accepted theories is that more efficient foraging by smaller males is the cause (Selander 1966, Reynolds 1972, Lundberg 1986, Hakkarainen and Korpimäki 1991, Hakkarainen et al. 1996, Hipkiss 2002, Sonerud et al. 2013, 2014a, Sonerud et al. 2014b). However, these conclusions have been reached in the absence of substantial experimental or observational data with which to demonstrate patterns at the population level. To my best knowledge, no data exist to directly document that smaller than average males of specific species increase their fitness in terms of lifetime reproductive success (Newton 1985, Laaksonen et al. 2004) through more efficient foraging. Two studies — coincidentally doing on the Boreal Owl nest box population in northern areas — have used field observational data to document correlations between the wing loading index of male owls and their prey delivery rates and ultimately the numbers of fledglings produced. These studies have shown that the effects of wing loading depend on environment conditions (Hakkarainen and Korpimäki 1991, Hakkarainen and Korpimäki 1995), specifically with variation in abundance of voles. These studies have documented that the male owls with reduced loading index provided higher prey delivery rate and produced more fledglings in years of low vole abundance. However, this pattern either does not exist in years of increasing vole populations, or is even reversed in years of peak vole abundance.

The findings of the above-mentioned studies are only in partial agreement with the results from my study, and mainly differ in two ways. Firstly, the results of my study have documented that lighter males that were provisioning the most typical broods (1–7 nestlings; for details, see below) delivered food at a higher rate than heavier males although they still raised the same number of nestlings. Thus, males with low body mass did not gain an advantage of enhanced nestling productivity (additionally, I have found the similar pattern between body mass of our male owls and fledgling productivity: 2002–2018, n = 100 males, $P < 0.01$, $F = 9.2$, $R^2 = 0.086$, $\beta = 0.294$; M. Zárybnická unpublished data). Secondly, my analyses on the quality of prey that the males brought to their nests revealed the additional effect of wing length on bird prey delivery that favoured the males with shorten wings, when these male owls were simultaneously of lower than average body mass, and simultaneously, the males with longer wings as long as they provided for only one nestling. More generally, the males with lower wing loading (i.e., lighter males with shorten wings, or the males with longer wings) brought a larger proportion of bird prey, and their nests produced fewer offspring. While I cannot offer a clear explanation for the differences between my results and those from previous research, I suggest that one potential reason is the differing conditions of the northern and temperate environment (for details, see Zárybnická et al. 2009, 2012, 2015e).

I conclude that the findings of my study do not provide clear support for the evolutionary advantage of small males in Boreal Owls, at least with respect to their foraging efficiency and reproductive success. Instead, my results suggest that the patterns that I have documented reflect changes in male size that result from, rather than causing, differences in provisioning of nests that I have documented. Below, I will elaborate on the reasons for my general conclusion, by: (1) summarizing how the presence of *Apodemus* mice, a genus not present further north, impacts the owl population that I have studied; (2) how year-to-year fluctuations in the abundance of *Apodemus* mice have revealed complex inter-male variation in the rate of prey delivery to nests; and (3) also how this variation affects types of prey brought to nests by different males.

The enhanced effect of Apodemus mice

My long-term examination of predator-prey relationships between the Boreal Owl nest-box population and small mammal communities have revealed multiple lines of evidence for the significant role of *Apodemus* mice in foraging and reproductive strategies of this owl in our study area. First, in this study, I have documented that *Apodemus* mice (comprised solely by Yellow-necked Mouse) were typically the most abundant rodent genera in spring trapping, although *Apodemus* abundance greatly varied over the time: the abundance of *Apodemus* mice varied from 0 to 19.5 individuals per ha, while *Microtus* voles only reached between 0.3 and 2.7 individuals per ha (the trapping event included three trapping nights, see methods). These findings are in agreement with our previous 25-year study (1991–2015) on inter-annual variation in small mammal communities (Zárybnická et al. 2017a) and 10-year study (1999–2010) on inter-annual variation in the Boreal Owls' diet (Zárybnická et al. 2013). Second, based on our 25-year study, we have documented the three-year cyclicity and the seasonal decline (from spring to autumn) of *Apodemus* abundance, but no significant among- or within-year variability has been found in *Microtus* voles (Zárybnická et al. 2017a). Third, using SNBoxes, I have found that the proportion of *Apodemus* mice in the owls' diet followed among-year and intra-seasonal abundances of this species in the field, but no such relationships were confirmed for *Microtus* voles. The similar results have been documented in our 10-year study performed based on pellet's analyses of the owls' diet (Zárybnická et al. 2013). Fourth, while nestling (this study) and fledgling (Zárybnická et al. 2013) productivity of the Boreal Owl significantly increased with the increasing proportion of *Apodemus* mice in the owl's diet, this relationship was not evident for *Microtus* voles. In summary, all these findings document that *Microtus* voles and *Apodemus* mice play different roles in foraging and reproductive strategies of northern and central European Boreal Owl populations (for details, see Korpimäki and Hakkarainen 2012, Zárybnická et al. 2015e), and emphasize that life history strategies of birds should be considered carefully under geographical variation (for details, see Martin 2004).

Predictors of provisioning rate

I have found that body mass of male owls — but not wing length — to be related to prey delivery rates: lighter males provided more prey items for the same number of the nestlings than heavier males. However, the interaction between body mass and brood size revealed that this relationship was the strongest when the male owls provided for only one or two nestlings, getting weaker with increasing brood size, with no effect of male mass for male owls provisioning six or seven nestlings, and even turning in an opposite effect when the males provided for eight nestlings (only one brood). Simultaneously, all males, regardless of their body conditions and the availability of *Apodemus* mice and *Microtus* voles, adjusted their prey delivery rate to nestlings' demands, as brood size and nestlings' age increased (see also, Zárybnická et al. 2012). Additionally, separated analyses on types of delivered prey revealed that males reduced their provisioning rate when delivering an increasing proportion of *Microtus* prey, while they increased their provisioning rate when increased *Sorex* prey delivery. However, these relationships only worked when *Apodemus* mice, and *Apodemus* mice and *Microtus* voles, respectively, were scarce.

These data suggest that variation in the mass of males was caused by variation in prey delivery rate that reflected nestling demands and food availability rather than the mass of males caused variation in amounts and types of prey delivered. In our study area, the most common brood sizes of Boreal Owls were between one and seven nestlings (97%, *n* = 191 broods, data from 1999–2018), and broods with eight nestlings only occur in the years of *Apodemus* mouse peak (Zárybnická unpublished data). The findings of this study suggest that the male owls, providing for the most typical brood size (1–7 nestlings), adjusted their prey delivery rates to nestlings' demands, but prey delivery rates varied among individual males, and the males with relatively higher provisioning rates had the lowest body mass. One of the reasons for increased prey delivery rates of the lighter males could lie in the different quality (nutritional energy) of the food that they provided. While the *Apodemus*, *Microtus*, *Myodes*, and avian prey weighted on average 22.4 g, 22.3 g, 19.4 g, and 20.4 g, respectively, the body mass of *Sorex* prey species averaged only 5.9 g. The result was an increased foraging effort of those males that delivered higher proportions of *Sorex* shrews, and conversely, reduced provisioning rates of those males that caught *Microtus* voles. I have found that at the time of food scarcity, when *Sorex* shrews were frequent prey, male Boreal Owl can provide up to 18 prey items (this study) or even up 24 prey items (Zárybnická unpublished data) per night for their nestlings and mates. At this time, the males also have larger home ranges (Kouba et al. 2017), broods suffer from higher nestlings' mortality (Zárybnická et al. 2015e), and nesting attempts often fail as a result of insufficient provisioning by the males (Zárybnická and Vojar 2013). A very different situation occurred when *Apodemus* mice peaked (2018) and the abundance of this rodent reached up to five-times higher abundances than average. My findings are that, at this time, the male owls can provide for up to eight nestlings and simultaneously to be heavier than average-weighing males. In summary, all these findings suggest that variation in body size of males did not advantage lighter males to provide for more nestlings through amounts or types of prey, but instead, that low mass of males (providing for the most typical brood size) resulted from a loss of mass that was a consequence of poor foraging efficiency.

Predictors of proportion of provided prey type

The analyses of separate prey groups have revealed the synergetic effects of body mass and wing length on the proportion of bird prey in the owl's diet. Contrary to bird prey, other prey groups did not display any relationships to the phenotype of the male owls. I have mainly found that the males with shorter wings provided bird prey with a higher probability than the males with longer wings, an effect only seen for lighter males (with below-average body mass), and the most evident effect was found for the lightest males with the longest wings, who delivered bird prey with up 40% probability. No effect of wing length on the probability of bird prey delivery has been found for heavier-than-average males. Additionally, the males with longer wings that provisioned only one nestling were about 15% more likely to deliver a bird prey to their nestlings than the males provided for more nestlings. Apart from the effect of male phenotype on bird prey delivery, I have found that the male owls reduced birds in their diet as nestling demands (both larger brood size and greater nestling age) increased, and along with among-year or intra-seasonal increases of *Apodemus* mouse abundance (see also, Zárybnická et al. 2013).

My findings support the idea that the capacity of the Boreal Owl males for increased manoeuvrability and more economical flight results from reduced wing loading, that can in turn increase foraging on birds (see also, Norberg 1970, Hakkarainen and Korpimäki 1991, Hipkiss et al. 2002b). It has been documented that relatively heavy birds with relatively small wings (i.e., high loading index or high wing loading) exhibit faster flight speeds and less manoeuvrability, while relatively light birds with relatively long wings (i.e., low loading index or low wing loading) increase their soaring ability and manoeuvrability (Norberg and Rayner 1987, Fernandez-Juricic et al. 2018). For sit-and-wait predators such as the Boreal Owl, feeding on bird prey requires more time and costs to searching for, hunting and loading of the prey that can weigh as much as the mass of the male owl itself (e.g. thrushes) than feeding on small mammals living on the ground and being readily captured (Newton 1979, Hakkarainen and Korpimäki 1991, Korpimäki and Hakkarainen 2012). I have found that the male owls decapitated bird prey with the similar frequency as those of rodents (19% vs 21–24%) before they had delivered it to their nests, as well as mean body mass of bird prey was similar to rodents' mass (20g vs 19–22g). These results suggest that the male owls probably were not overloaded when they delivered bird prey to their nestlings. At the time of food scarcity, Boreal Owls feed on various bird species, although they most frequently take finches, thrushes, tits, and Yellowhammers (see Chapter 3.1). These prey species often exhibit conspicuous behaviour, for example, they sing at exposed or elevated points till late evening and from early morning, respectively. At this time, nocturnal Boreal Owl males start and terminate, respectively, their daily activities (Drdáková-Zárybnická 2008, Zárybnická et al. 2012) and songbirds can be relatively easily available to them. Simultaneously, using SNBoxes, I found that nestlings comprised up to 30% of bird prey, and capture of nestlings would likely require increased costs in searching for bird nests in forest habitats rather than in increased costs in fast and agile flying to pursuit birds. These findings support the idea that Boreal Owls profit from the increase of their soaring ability and manoeuvrability when feed on bird prey. In my study, this effect has been mainly documented at the time of *Apodemus* mouse scarcity in males who exhibited lower wing loading and provided for reduced brood size.

3.3 Conclusion

While I did identify associations between male size and provisioning behaviour, most of these associations related to male mass — an aspect of male size that can change rapidly — rather than to the less variable aspects of size represented by wing length. My findings suggest that the differences in male size represent changes in male mass that reflect the energetic costs to the males experiencing differences in availability of their preferred prey. Thus, variation in male mass was largely a consequence, rather than a cause, of differences in provisioning behaviour that were associated with fluctuations in abundance of their preferred *Apodemus* prey.

With the small male hypothesis not explaining the reverse sexual size dimorphism in Boreal Owls, alternative explanations for reverse sexual size dimorphism need to be examined. These alternative hypotheses involve aspects of sex-role differentiation other than foraging, such as egg productivity, the differentiation of parental care and duties, incubation and brooding bouts, feeding and dismembering prey, brood reduction, sibling competition, and many others (for details, see Selander 1966, Reynolds 1972, Lundberg 1986, Hakkarainen and Korpimäki 1991, Hakkarainen et al. 1996, Hipkiss 2002, Sonerud et al. 2013, 2014a, Sonerud et al. 2014b). I believe that the data from video recordings at nests will have a valuable role to play in examination of these other hypotheses.

4

Using Automated Data Collection for Environmental Education

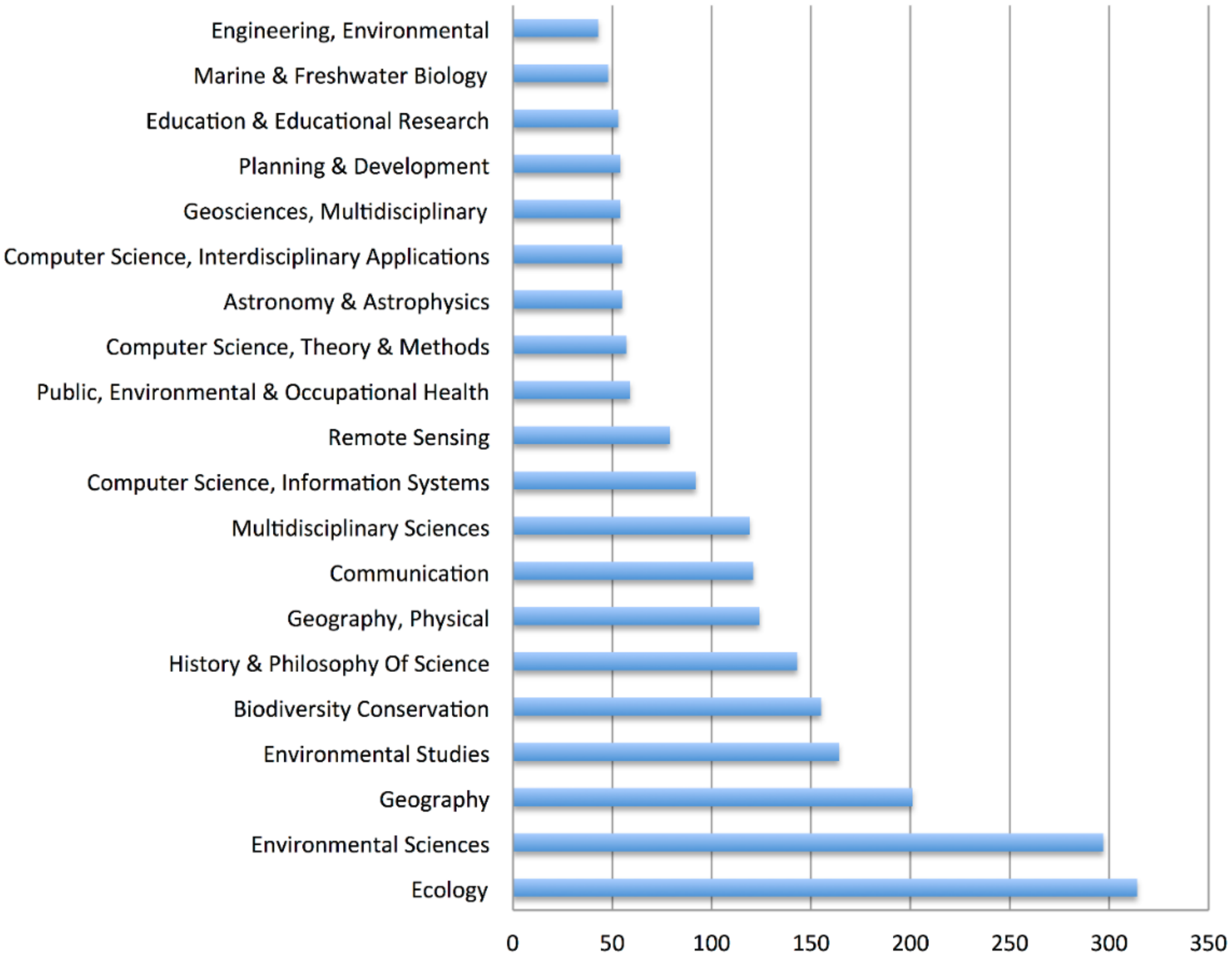
Case study:
Birds Online project

In this chapter, I document the potential of *IoT technology* to be used as an effective tool for *Citizen Science* that is designed to engage the public in research activities. Specifically, I introduce the *Birds Online project* that our team has conducted as a Citizen Science project which has used the Internet-connected SNBoxes to (i) engage the public in environmental education through direct observation of nesting birds that serves to disseminate knowledge about bird lives and their behaviour; (ii) disseminate avian and environmental education resources to multiple audiences for the purposes of both formal and informal school education, as well as university education; (iii) engage the public in field work through the installation and maintenance of the technical devices; and (iv) collect high-quality research data through the automation of much of the data collection process while achieving educational objectives.

4.1 What is Citizen Science?

Citizen Science is public participation in organized research efforts, and Citizen Scientists are people who have chosen to use their free time to engage in some aspect(s) of the scientific process (Dickinson and Bonney 2012). Citizen Science projects involve the public in authentic research alongside professionals, and thus they can provide both educational benefits for the public and large amounts of high-quality data for researchers. Current implementations of Citizen Science projects most often mobilize (“crowd source”) volunteer participants to assist with the collection and classification of observations. However, Citizen Science projects can also involve communities in designing projects and creating data to influence policy and promote political decision-making processes (Kullenberg and Kasperowski 2016). Topics of Citizen Science vary from Environmental Science through Geography, Communication, Computer Science, Geoscience, Engineering, Astronomy to Education Science (Fig. 32). A substantial part of the research has also emerged through geographic information research, where citizens participate in the collection of geographic data (See et al. 2016, Brown et al. 2019). The largest proportion of Citizen Science is focused on Environmental Science, Ecology, and Biodiversity Conservation (Fig. 32), where citizens mostly participate in data collection and classification (Kullenberg and Kasperowski 2016). The most productive projects in terms of the number of scientific outputs have focused on ornithology (e.g., the Common Birds Census, North American Breeding Bird Survey, eBird) (Kullenberg and Kasperowski 2016).

Figure 32. Web of Science Categories sorted based on the number of publications generated by Citizen Science (n = 1935) according to Kullenberg and Kasperowski (2016).



4.1.1 Public engagement

As noted above, the public engages in Citizen Science projects through various activities, including defining questions, gathering and disseminating information, designing methodologies and tools, data analysis, and computing (Bonney et al. 2009; Silvertown 2009; Gaydos and Squire 2012). Most often, participants are engaged in Citizen Science projects through a *field-based* or an *online-based* approach. The field-based approach, found in about 58% of Citizen Science projects, allows high volumes of data to be collected over large temporal and spatial scales, most often based on observing, mapping, measuring, installing sensors, or maintaining sensor infrastructure. The online approach, found in about 25% of Citizen Science projects, usually uses a digital base for running computer programs, digital gaming, video data analysis, or disseminating project's conclusions. Some Citizen Science projects (17%) use both the field and online approaches (Bonney et al. 2009; Fritz et al. 2017).

An example of a successful field-based Citizen Science project is eBird, developed and maintained by the Cornell Lab of Ornithology, that engages a vast network of human observers to report bird observations (Pimm et al. 2014, Amano et al. 2016). This project includes 100,000 participants in bird monitoring, with outputs of the project contributing to basic science, conservation, and public policy (Sullivan et al. 2014). A similar field-based Citizen Science project, called eMammal, incorporates volunteers to deploy hundreds of camera traps for mammal monitoring across the USA and to regular uploading the photos from these devices (McShea et al. 2016). Another example of a successful digital-approach Citizen Science project is Zooniverse, for which participants classify or interpret audio files, videos, or pictures, such as millions of images of galaxies, moon craters, organisms, or animal behaviour (Bonney et al. 2009; Simpson et al. 2014). Finally, the global xeno-canto Citizen Science project engages people in collecting and freely distributing bird songs from across the globe (Vellinga and R. 2015). Regardless of the type of approach, most Citizen Science projects require a community with some domain-specific knowledge. For example, bird watchers engaged in the eBird program are expected to identify birds that they observe in the field (with the assistance of a mobile application), and field volunteers in the eMammal project are asked to tag the content of the photos before uploading. Other projects can require participants to provide infrastructure (e.g., home computers) to do some extracurricular work when the machines would otherwise be idle (Hand 2010). As a result, it can be challenging to participate in and receive educational benefits from Citizen Science projects for a part of the community; e.g., disabled and disadvantaged people, children, or the elderly.

4.1.2 Motivation of participants

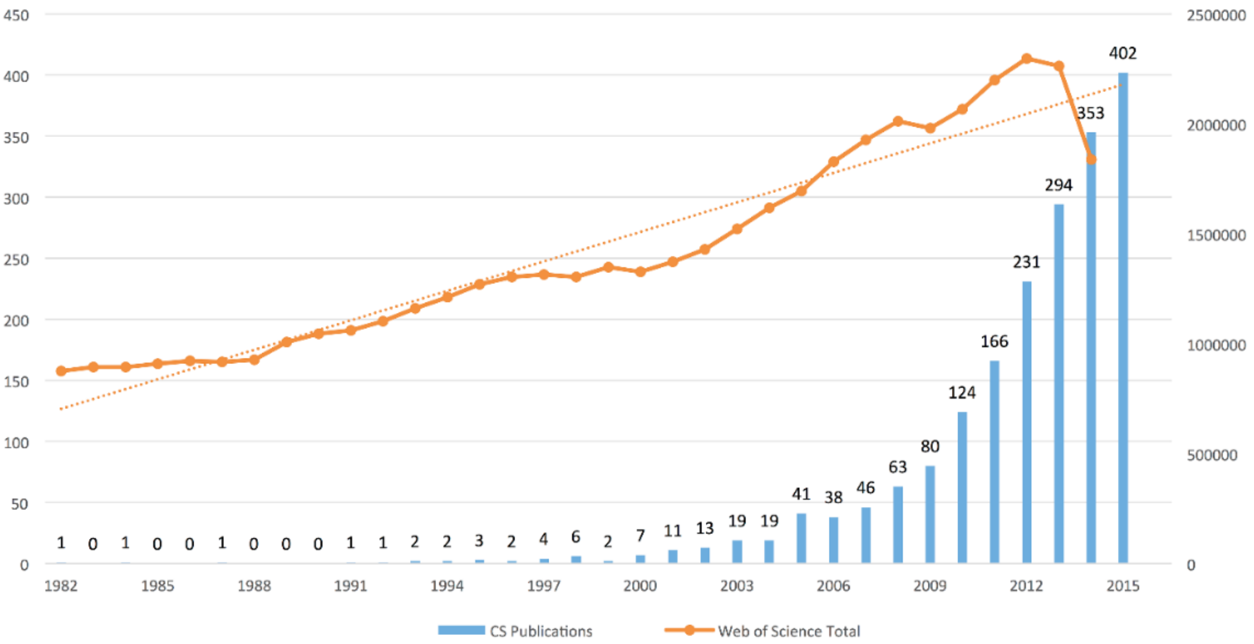
The key to the success of Citizen Science projects is the motivation of the volunteers based on their feeling that their activities are beneficial both to themselves and more broadly. Professional scientists and volunteers participate in scientific endeavours for a variety of reasons; professional scientists want to advance science and further their own professional career, and volunteers often participate in a project's activities as a matter of interest, curiosity, feeling useful, and commitment to conservation and related educational efforts (Fritz et al. 2017). Volunteers are motivated by a complex set of factors that change dynamically throughout their cycle of work on scientific projects, and this motivational framework is strongly affected by personal interests as well as external factors such as attribution, outputs of the project, personal benefits, and acknowledgment. Identifying the pivotal points of motivational shift and addressing them in the design of citizen-science systems plays a key role in improving collaboration between scientists and volunteers (Bonney et al. 2014; Fritz et al. 2017).

An excellent example of how scientists can motivate the public to participate in data collection is seen in the eBird project. This project provides tools — a mobile and web application — to promote hobby activities of amateur ornithologists and the public to a scientific effort. Based on participants' observations, scientists gather information on species occurrence, migration timing, and relative abundance at a variety of spatial and temporal scales (Sullivan et al. 2014). Each of eBird's observers can enter bird lists to monitor bird species in their own area or to map overall abundance of a species on private premises over time, to get a direct connection to citizen scientists in the local community, state, and all over the world, to create their own eBird Hotspots, and to gain data that can contribute significantly to the decision-making process when considering land for protection (for details, see http://www.birds.cornell.edu/landtrust/benefits-of-ebird/). Similar Citizen Science projects, such as iNaturalist (Heberling and Isaac 2018), Atlas of Living Australia (Belbin and Williams 2016), or Biolog (Zárybnický et al. 2015), have been designed and developed for more restricted geographical areas, different taxa, and purposes.

4.1.3 Scientific benefits

Although scientific outputs of Citizen Science projects (measured as the number of publications generated by Citizen Science based on the Web of Science database) have boomed over the past decade as a result of an emergence of digital platforms (Fig. 33; Kullenberg and Kasperowski 2016), the practice of Citizen Science itself is much older. Previously, volunteer contributors have not been made visible in scientific articles to a wide extent and most communications were maintained via personal paper correspondence (Šťastný et al. 1987, 1996, 2006, Hagemeijer and Blair 1997, Schmid et al. 1998, Sikora et al. 2007). This changed with the introduction of digital platforms. Three general developments have been suggested as causing the great explosion of Citizen Science in the last decade. First, the existence of easily available technical tools, such as the Internet and smartphones, has facilitated the dissemination of information about projects and data collection from the public. Second, there has been increasing awareness among professional scientists that the public represents a free source of labour, skills, computational power, and even finance. Third, some grant agencies (e.g., the National Science Foundation in the USA) have encouraged or even required that projects undertake project-related science outreach to make sure that the public will appreciate the value of spending taxpayers' money (Silvertown 2009; Fritz et al. 2017).

Figure 33. Growth of Citizen Science publications (*n* = 1935 publications) compared to the Web of Science total publications according to Kullenberg and Kasperowski (2016).



4.1.4 Educational benefits

Citizen Science projects can provide significant educational benefits for the public, as the volunteer contributors learn about the process of scientific investigation, deepen their relationship with their environments, interact with experts, and improve their skills (Borden et al. 2013). More specifically, the participants in ecological and environmental projects can increase their abilities to identify habitats and organisms, to improve their knowledge about the biology and ecology of plant and animal species, to learn about local environments, to make measurements, to collect field data following specific protocols, and to sample consistently over time. Additionally, the participants can gain skills in reading and interpreting graphs, drawing conclusions from evidence, communicating results, raising new questions as a basis for new study designs, and weighing the pros and cons of various research designs, data collection methods, and outcomes (Bonney et al. 2009; Bonney et al. 2014).

4.1.5 Challenges for the future

Although Citizen Science offers a promising approach and many long-term and well-established Citizen Science projects have provided unique educational and research outputs (see above), the full potential of Citizen Science has not yet been realized. For example, Citizen Science projects often lack synergy with the local education system and insufficiently emphasize synergies between environmental education and science education (Wals et al. 2014); high-quality collaboration among scientists, project organizers, government institutions, and the public is rare (Kobori et al. 2016); volunteers can gather data of differ quality or limited validity (Silvertown 2009; Hunter et al. 2013); project methods cannot be usually implemented across society because they focus on a narrow circle of volunteers or skilled amateurs; and project outputs are often presented unclearly to the public or even to the volunteers involved (Silvertown 2009; Bonney et al. 2014). At this time of increasing urbanization, disconnection of people from the natural world, and global digitalization (Balmford et al. 2002), developing new approaches and methods can be essential for the impact of ecological and environmental Citizen Science projects on the public and dealing with the above-mentioned weaknesses.

4.2 The Birds Online project

The Birds Online project that our team has conducted as a Citizen Science project aims to engage the public in research activities and environmental education through the use of SNBoxes to monitor nesting birds that occupy urban areas. More specifically, we have used our purpose-designed Internet-connected camera systems (for details, see Chapter 2.4.2) for both live and retrospective monitoring of cavity-nesting birds and the collection of audiovisual and ancillary data, while engaging people in bird watching and the installation and maintenance of SNBoxes on the hosting premises (Fig. 34; Zárybnická et al. 2017d). To achieve our educational aims, we have gradually deployed and remotely operated dozens of SNBoxes across the Czech Republic, but also in Poland and the USA (Fig. 35, Chapter 4.2.1) in which we monitored more than 150 nesting attempts (Chapter 4.2.2). To introduce bird watching to the broadest audience, we have cooperated with the public, mainly installing SNBoxes at hosting premises that are educational institutions, as long as they provide a site, Internet connection, and mains power for the SNBox. Every new SNBox installation has been published on the project website *www.birdsonline.cz* (Chapter 2.4.2) and referenced by an icon on an interactive map (Fig. 35). Each SNBox has provided live streams, listed all video recordings available for playback (Fig. 36) that have been categorized by the date and the nesting species, and provided nest statistics. Video recordings from all SNBoxes have been transmitted automatically every day and published with a one-day delay. Anybody can watch or download any video recording (for details, see Kubizňák et al. 2019).

Figure 34. The functional scheme of the Birds Online project, with direct benefits for the public and for researchers. For details, see Zárybnická et al. (2017d).

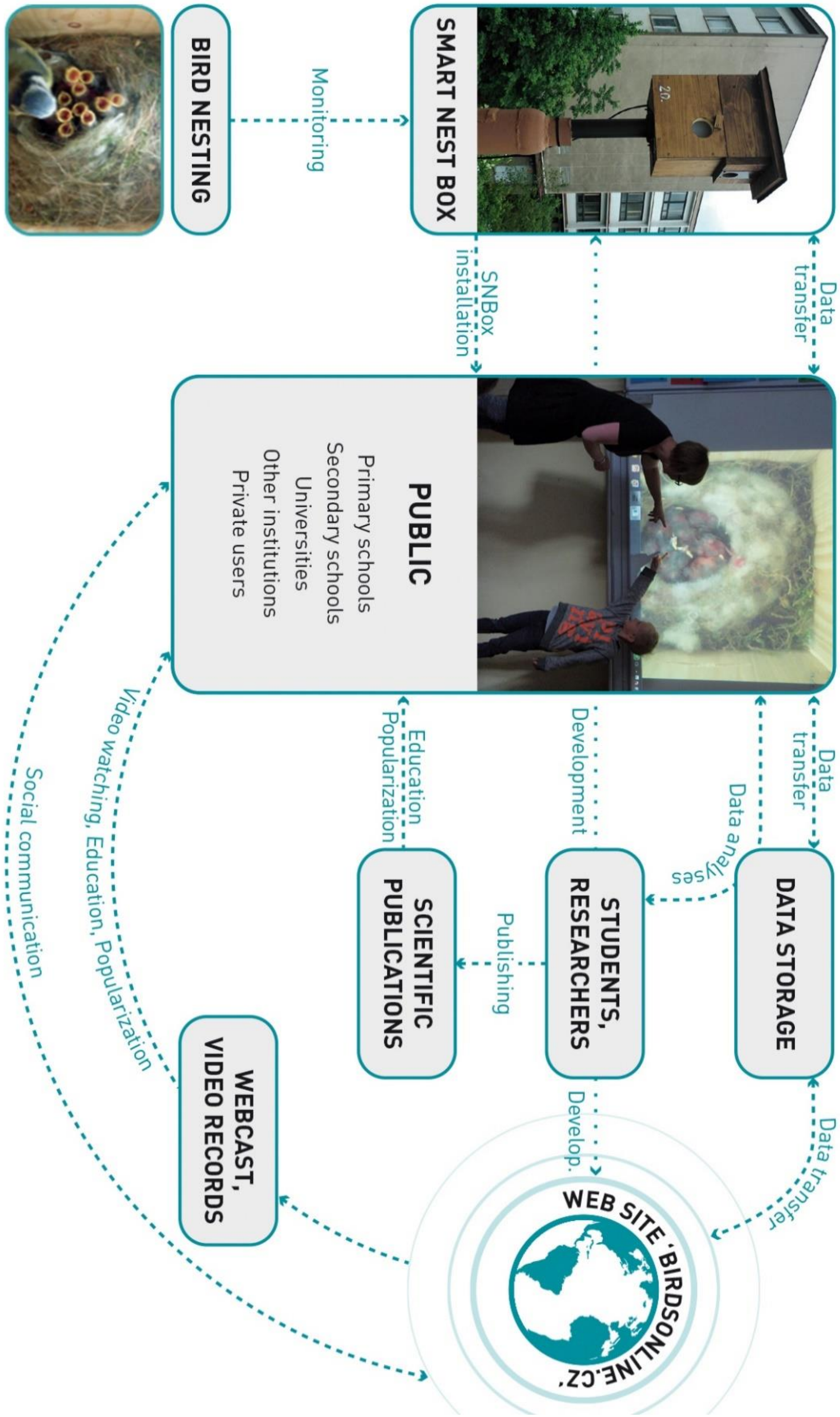


Figure 35. The interactive map of the SNBoxes installed within the Birds Online project available on the project's website www.birdsonline.cz.

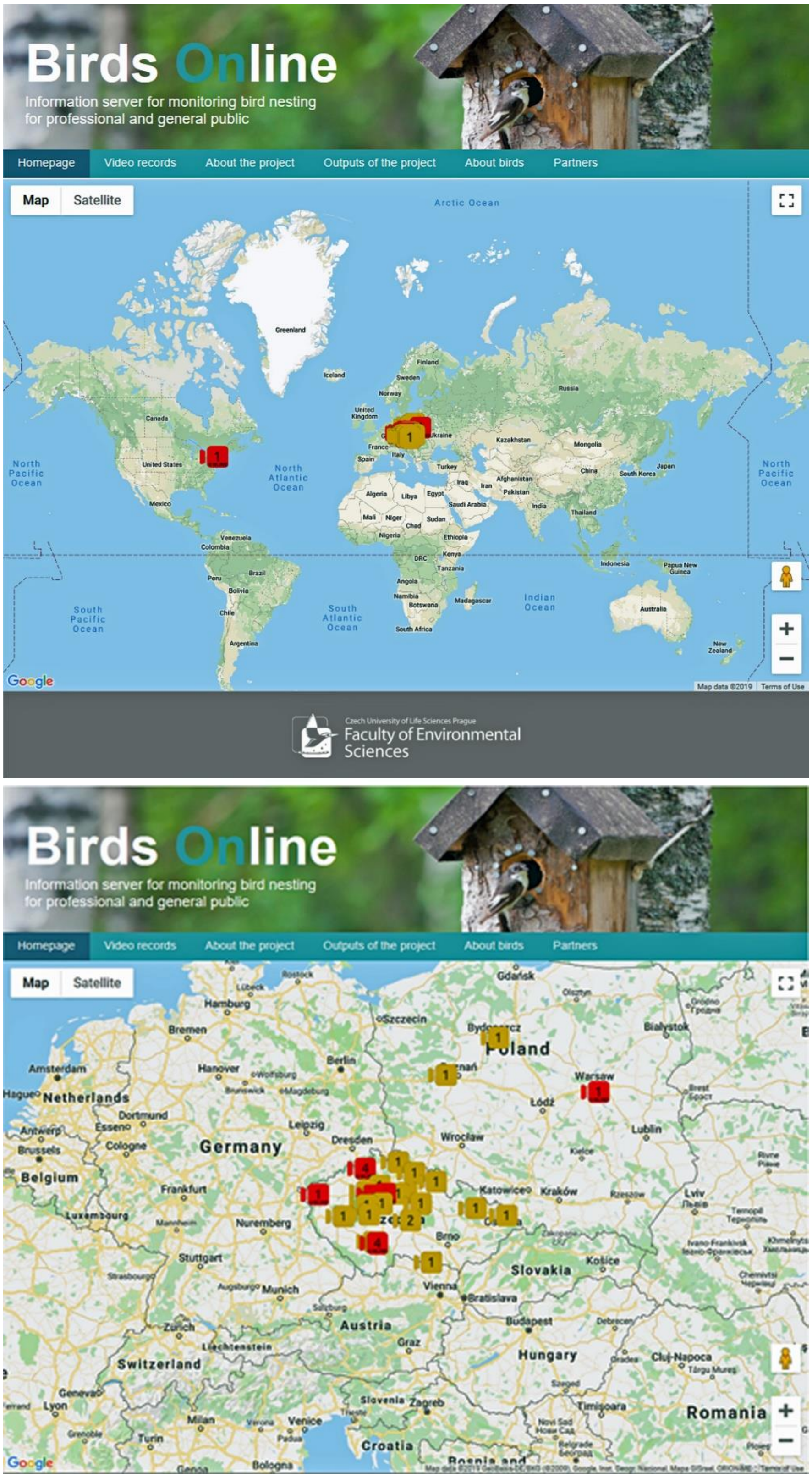
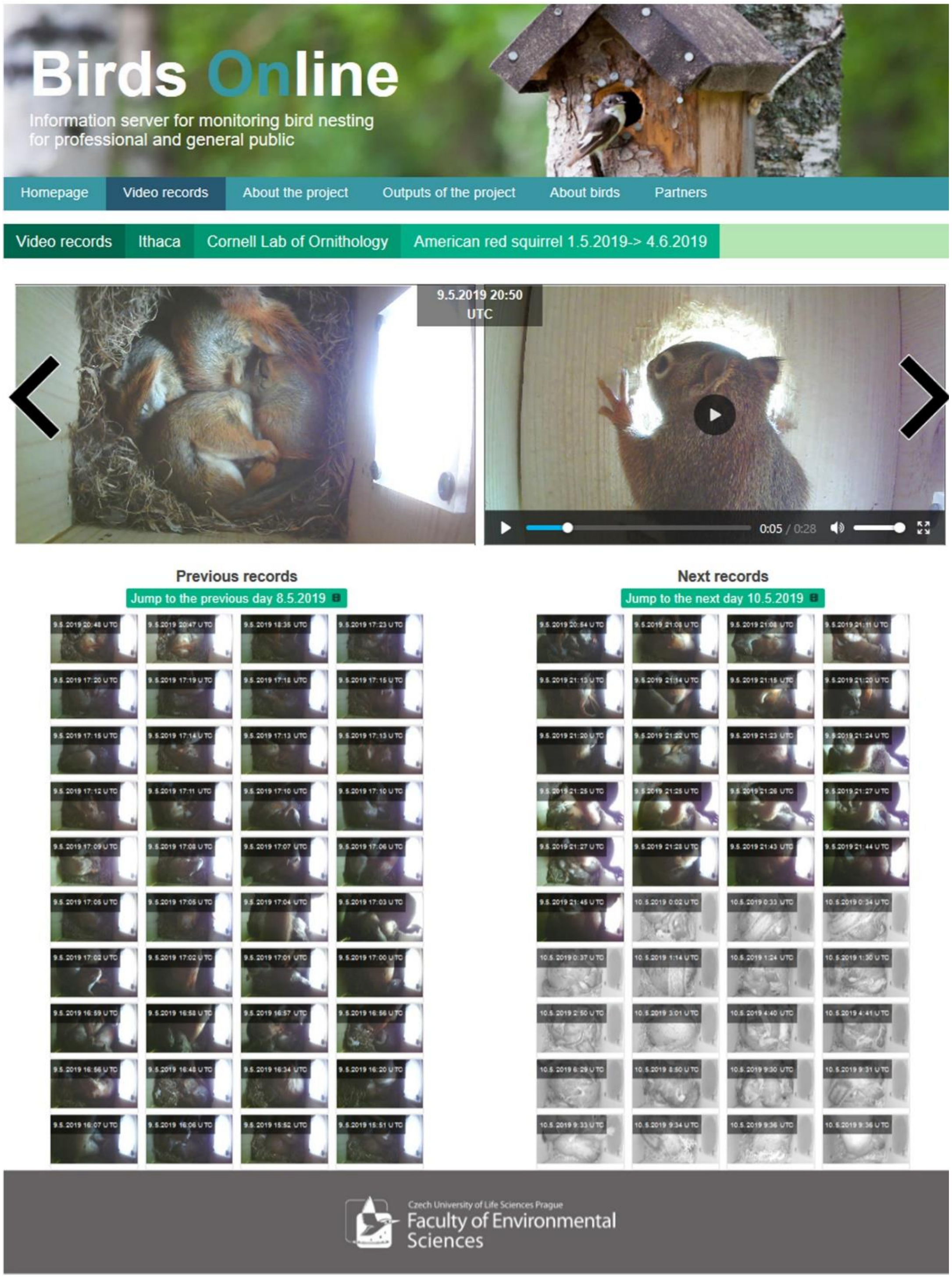


Figure 36. Examples of video recordings of the American Red Squirrel (*Tamiasciurus hudsonicus*) young available for playback on the Birds Online project's website www.birdsonline.cz, collected by the SNBox located at the hosting premises of the Cornell Lab of Ornithology in Ithaca (USA). Videos were recorded using two commercial colour cameras embedded in the SNBoxes (the first camera was placed on the back of the SNBox to capture images of the nest box entrance, and the second camera was located on the ceiling of the box to capture images of nesting area).



4.2.1 SNBox deployment

Between April 2016 and October 2019, we installed and remotely operated a total of 57 Internet-connected SNBoxes. We designed these boxes as nest sites for passerine birds (*n* = 52 SNBoxes), Common Swift (*Apus apus*) (one SNBox), and Little Owl (*n* = 4; note that these SNBoxes were funded by the Czech Society for Ornithology). All the SNBoxes have been located on private premises in villages or towns and work online. Of this total, 33 SNBoxes were equipped with the model 2.0 system and 24 with the model 3.0 system (for details, see Chapter 2.4.2). We deployed the SNBoxes gradually throughout 2016–2019 (cumulatively, 22 SNBoxes in 2016, 33 in 2017, 51 in 2018, and 57 in 2019) in Czechia and Poland across a 140,000 km^2 region (Fig. 35), and one of the SNBoxes was also placed at the Cornell Lab of Ornithology in the USA. Over time, the 57 SNBoxes have been placed at a total of 70 hosting premises (some SNBoxes were moved once or twice). Of the hosting locations, there were 44 schoolyards (preliminary, elementary, middle, high, and special schools), 15 private gardens, four hospital grounds, four phenological gardens, two university grounds, and one zoological garden. SNBoxes were most often installed on trees (*n* = 57 localities), and less commonly on loggias of blocks of flats (*n* = 4), windows or walls of the buildings (*n* = 7), and electric poles (*n* = 2) at a height of 2–20 m above the ground (mean ± SD, 5.7 ± 2.6 m). The surrounding environments of the nest boxes (buffer radius of 20 m) on average consisted of 54.9% (SD = 23.8) vegetation cover comprising shrubs, trees, flowerbeds, and grass areas, and 45.1% (23.8) built-up areas.

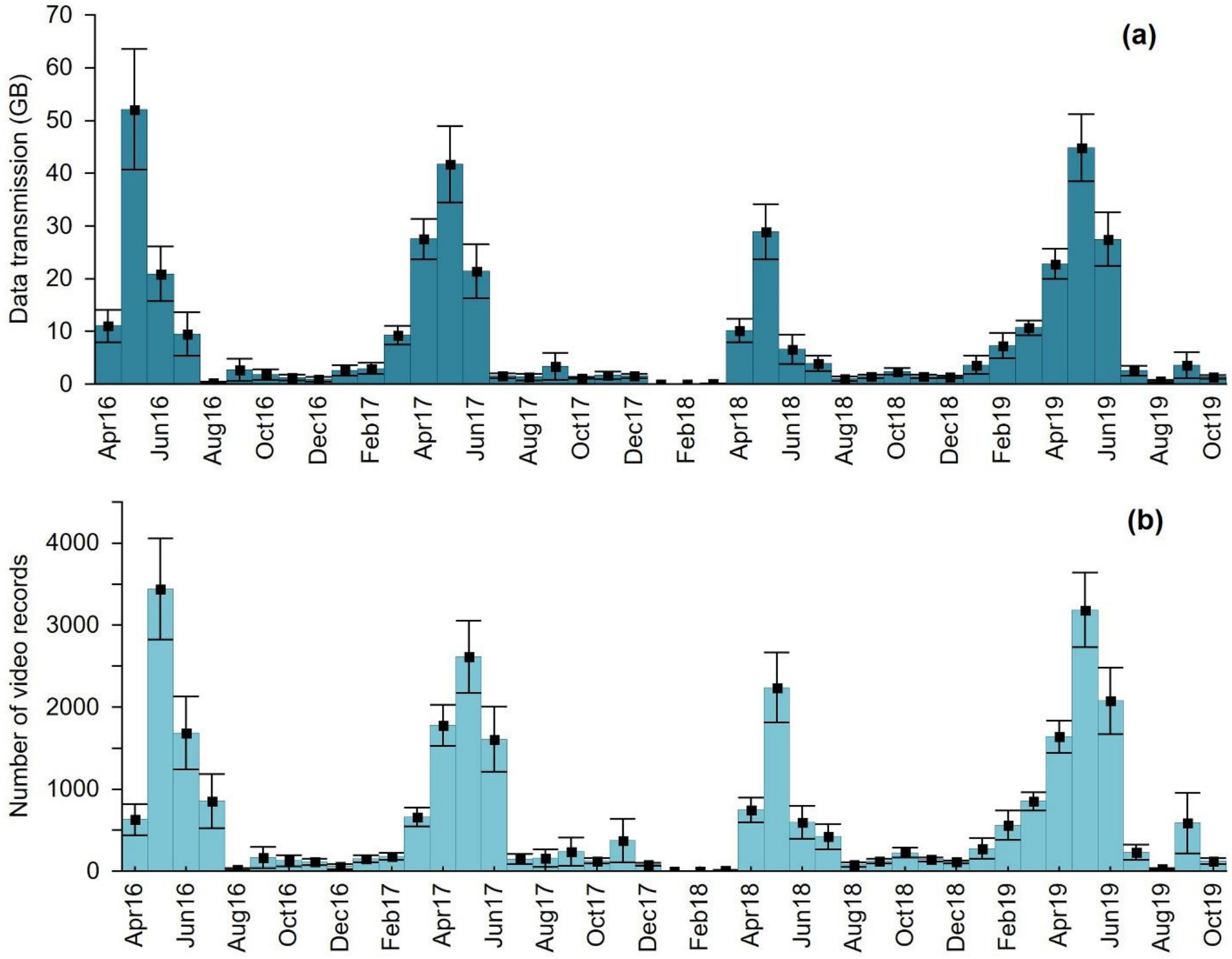
4.2.2 SNBox occupancy

We recorded a total of 155 bird nesting attempts and one mammalian brood in the 57 boxes (median, 25–75 %, min–max: 2, 1–4, 0–7 events per box) across four breeding seasons. The most frequent nester was Great Tit (*n* = 104 nests; Fig. 6), followed by Eurasian Tree Sparrow (*Passer montanus*) (*n* = 25 nests; Fig. 6), Common Starling (*Sturnus vulgaris*) (*n* = 18 nests; Fig. 6), Eurasian Blue Tit (*Cyanistes caeruleus*) (*n* = 3 nests; Fig. 6), Little Owl (*n* = 3 nests; Fig. 6), Common Redstart (*Phoenicurus phoenicurus*) (one nest; Fig. 6), and Common Swift (one nest; Fig. 6). We also recorded one individual of American Red Squirrel (*Tamiasciurus hudsonicus*) that reared young in the SNBox located in the USA (Fig. 6, 36). Other species, such as Eurasian Wryneck (*Jynx torquilla*), White Wagtail (*Motacilla alba*), House Sparrow (*Passer domesticus*), Eurasian Nuthatch (*Sitta europea*), Great Spotted Woodpecker (*Dendrocopos major*), Carolina Wren (*Thryothorus ludovicianus*), and Flying Squirrel (*Glaucomys* sp.) visited the boxes. No bird nesting was recorded between September and February, although, birds and mammals visited SNBoxes sporadically for a short time or regularly (e.g., using boxes as overnight roosting locations) throughout the whole year.

4.2.3 SNBox data acquisition

From April 2016 to October 2019, the 57 SNBoxes were in operation for 1997 months (34.4 ± 9.3 months per SNBox). A total of 1.3 million short video recordings (each record usually 30 s in duration) totalling 16.5 TB were remotely transmitted from the SNBoxes to the university server located at CULS in Prague (for details, see Chapter 2.4.2). On average, 662.5 video recordings (SD = 1671.8, min = 0, max = 16,863) and 8.8 GB (SD = 22.2, min = 0, max = 200.2) in size were transmitted from each box per month (Fig. 37).

Figure 37. Rates of data acquisition using SNBoxes; (a) mean monthly volume of data (GB) and (b) the number of video recordings transmitted from each SNBox to the university server between April 2016 and October 2019. Mean ± SD are shown.



4.2.4 Educational benefits

The installation of SNBoxes at hosting premises and bird watching available through live streams or video recordings on the website of the Birds Online project have allowed for three main types of educational activities aimed to the public. First, the presence of the SNBoxes provided exposure to field education through participants physically checking the content of the SNBox, including bird nesting and the technical devices. Second, digital educational resources were provided through the observations of birds' nests on digital screens. Third, the presence of SNBoxes and observations of videos from these boxes provided the motivation for practical educational activities, as students, their teachers, and other engaged people producing a wide range of handcrafted products. The project objectives have strived to facilitate all three approaches through all-level formal and informal education, including 3–6-year-old children (preschools), 7–11-year-old students (elementary schools), 12–15-year-old students (middle schools), and 16–19-year-old students (high schools), as well as to make use of the project's outputs for the purposes of university education by engaging bachelor, master, and PhD students.

Field education

In the case of the Birds Online project, the benefits of field education lie in the direct contact of participants with the SNBox. The participants that were directly involved in the SNBox installation had the advantage, compared to the non-participants, of having a nest site in their own schoolyard or garden. This allowed participants, and mostly teachers and students of engaged educational institutions, to develop tight relationships with the local environment through direct observation of nesting located in their SNBoxes and physical checking the content of the SNBox (Fig. 38c–i), including nest materials, eggs, and young. The location of the SNBox in schoolyards also allowed students to be introduced to the wooden construction and the technology of the SNBox (Fig. 38c–i). These activities were applicable to, and adjustable for, all ages of students.

Digital education

The main advantage of IoT technology applied in the Birds Online project lies in real-time or retrospective watching of animal activities in each of the SNBoxes that were filmed throughout the day (and night) and across the entire year. Everybody (i.e., the project's participants and non-participants) can remotely enjoy watching the events that have been happening in the SNBox and use audiovisual outputs. In all-level schools, teachers have introduced freely available live video streams or records of nesting birds on interactive screens or laptops into lessons on the environment and biology as a stimulating visual teaching aid (Fig. 39, 40). Additional to bird nest watching, teachers have used interactive screens to encourage preschool children to practice basic counting or drawing bird silhouettes (Fig. 41).

Practical education

The most varied form of benefits from the Birds Online project, applicable at all-level schools, lie in extended activities related to bird nest watching. Such activities can cross a wide spectrum of subjects and lessons, including biology, environmental science, ecology, art, music, writing, physics, mathematics, informatics, media studies, sociology, grammar, literature, science, and practicing handicraft skills. For example, young schoolchildren have kept diaries of daily bird nest activities, produced bird books, created pictures of birds and bird life (Fig. 42), written stories about the birds they observed (Fig. 43), sung songs, read bird stories, and created various handcraft objects related to birds, their nests, and behaviour (Fig. 44). Teachers have decorated their classrooms with the children's products and work, as well as used observed biological information for producing entertaining presentations (Fig. 45) and outdoor and classroom activities (Fig. 38a–b, 46). Apart from gaining biological knowledge, students of advanced degrees have developed their technical skills. For example, students at middle (12–16-year-old students) schools have used video recordings to produce short video clips on bird nesting, or they have built standard wooden nest boxes to deploy them in their schoolyards (Fig. 38j). Finally, students in more advanced grades at vocational training schools have developed their technical skills in materials, machining, and producing documentation during the course of making wooden boxes used for the SNBox system.

A special potential for disadvantaged students

Enormous potential of the audiovisual outputs of the SNBoxes has been found in special schools working with disabled and disadvantaged students. Teachers of such students have appreciated the opportunity to incorporate direct observations of nesting birds during lessons on biology and the environment, and to use the knowledge gained to practice handcraft activities, similar to the activities of students at standard schools (Fig. 46).

Homeschooling

Last but not least, home-schooled students have also engaged in the Birds Online project's activities. These students have learned about bird behaviour and ecology through direct observation of birds nesting (i.e., digital education), and were incorporated into the manual processing of video content to gain biological information on bird nesting. Such students have practiced working with a database and summarizing data using basic statistics, as well as interpreting the biological findings at the Czech Ornithological Conferences for Young People and introducing their participation in the Birds Online project on Czech television (Fig. 47).

Informal education

Audiovisual outputs from the SNBoxes have also been efficiently used in a range of informal education settings. More specifically, over 60,000 unique individuals or groups from over 100 countries have viewed the live streams or recorded videos of the Birds Online project (based on Google Analytics, Kubizňák et al. 2019). Simultaneously, the project has also supported the popularisation of science by presenting an example of effective collaboration between scientists and the public via social media, radio, TV, and news programs (for details, see *www.birdsonline.cz*, Zárybnická et al. 2017d).

University education

University-level students, i.e., the students of bachelor's, master's, and PhD degrees, have also been involved in the Birds Online project. More specifically, a total of 26 students of bachelor's and master's degrees and two PhD students defended their theses related to the Birds Online project between 2016 and 2019. For example, students of environmentally administrative study programs manually processed the content of video material to gain biological information on breeding biology, food ecology, and parental behaviour for the purpose of creating material for their bachelor's theses. Master students of environmentally administrative and applied ecology study programs have usually participated in both the organization of the project and the evaluation of biological information from multiple nests. Examples of master's theses include topics on the dietary ecology of Great Tit and Common Starling (Hradcová 2019) and the evaluation of nest attendance by Great Tit parents in relation to the phase of incubation and weather conditions (Kerdová 2019). Additionally, stored video materials encompassing over 1.3 million recordings have been used by bachelor and master students as a source for the development of machine learning algorithms for automated extraction of biological information from the videos (Havlůj 2018; Šuma 2018).

PhD students have played substantial roles in project implementation, technological development, and data evaluation. Mainly, Petr Kubizňák designed and developed the complex technology of the SNBox — he developed the stand-alone SNBox within his master's degree (Kubizňák 2014) and the Internet-connected SNBox within his PhD degree (Kubizňák 2019), while Jiří Šindelář applied SNBoxes for the Boreal Owl nest monitoring during a four-year period in the Ore Mountains within his PhD degree (Šindelář 2019).

Figure 38. The outputs of the Birds Online project. An example of improving biological knowledge and technical skills of all ages of students: (a) indoor desk activities of preschool children; (b) indoor computer activities of 16–19-year-old students; (c–g) outdoor activities of students and preschool children related to improving their knowledge about bird lives and the SNBox technology; (h–i) checking the SNBoxes and cleaning nest material by 12–19-year-old students; and (j) producing the standard wooden nest boxes by 12–15-year-old students.

(e) (f)

(g) (h)

(i) (j)

Figure 39. The outputs of the Birds Online project. An example of the use of live video streams of bird nesting on projection screens during lessons on the environment and biology in elementary schools (7–11-year-old students).

Figure 40. The outputs of the Birds Online project. An example of the use of live video streams of bird nesting on projection screens during lessons on the environment and biology in elementary schools (7–11-year-old students).

Figure 41. The outputs of the Birds Online project. An example of the use of live video streams of bird nesting projecting on interactive screens to encourage preschool children to practice basic counting and drawing bird silhouettes of the incubating bird.

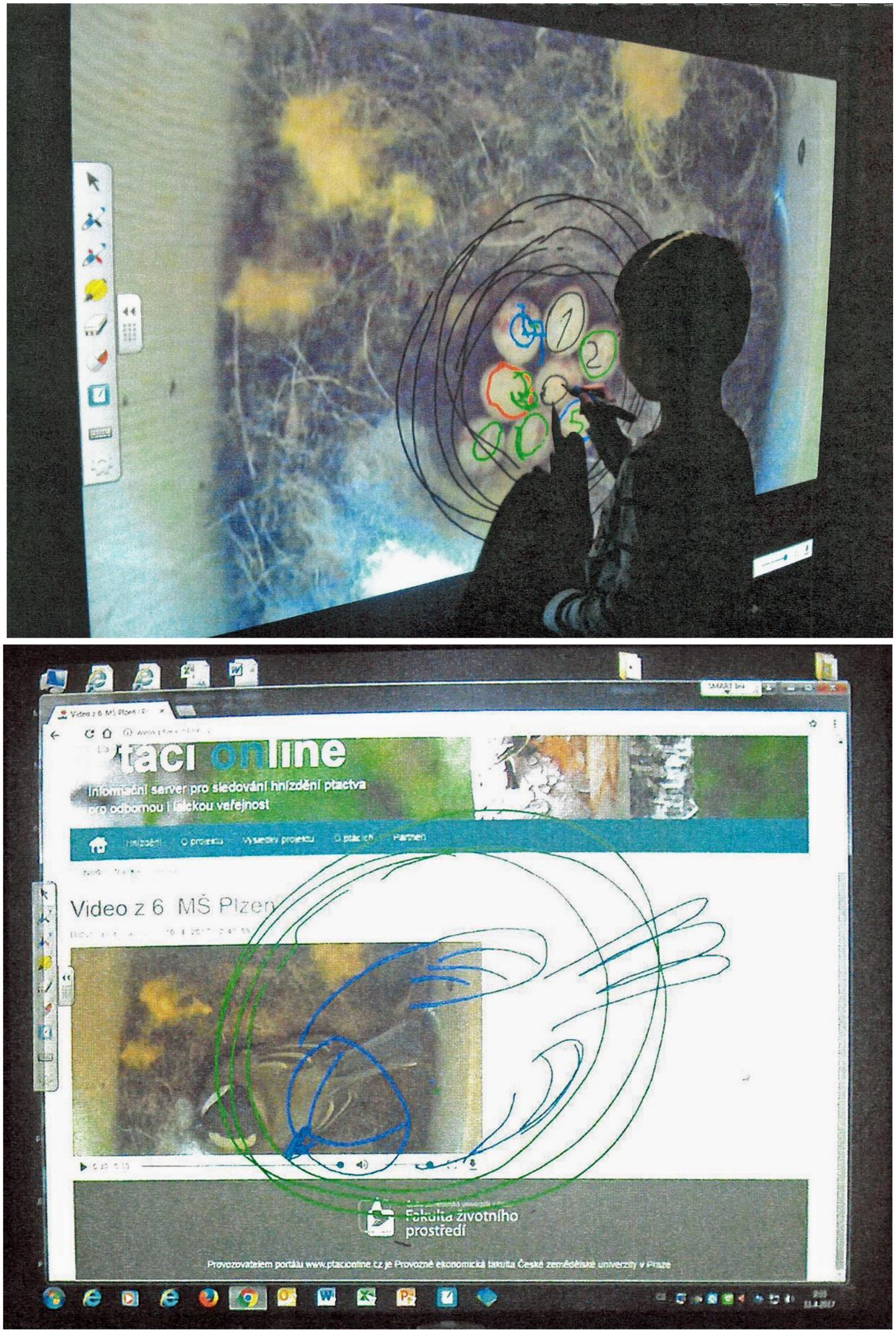


Figure 42. The outputs of the Birds Online project. An example of the pictures created by the 7–11-year-old students from elementary and special-needs schools.

Figure 43. The outputs of the Birds Online project. An example of the bird stories created by the 7–11-year-old students from elementary schools.

Sýkora koňadra

Sára . LoPatová

Byla jednou sýkorka a sameček a ty měli 4 vajíčka. Za 10 dní se jim vylíhla 3 miminka. Maminka a tatínek se už dlouhou dobu báli, že se to poslední vajíčko už nevylíhne. Tak zavolali doktora. A ten říká, no, no nevím co to je za nemoc. Tak řekl počkejte si do druhého dne. No a dočkali se. Počkalise pár dní a už jsou velké jako skoro maminka. A tatínekanapadlo, že se budou stěhovat. Tak letěli do Afriky, tam se ubytovali. Ale asi za měsíc se jim stýskalo po Čičově. Tak si řekli, že se vrátí zpátky do Čičova. A žili šťastně až do smrti.

Sýkoří samec Petr

Petr byl zdatný samec. Byl sám a chtěl se oženit. Měl hodně Samiček. Proto si mohl vybrat. Proto si to nechal uležet v hlavě, jakou si vybere? Mohl si vybrat Zuzku, Evu, Šárku. Druhý den měl nápad. Uspořáda sýkoří pětiboj. Pozval samičky. Samičky závodily jako divoké čertice. Vyhrála Šárka. Petrovi se líbila. A tak spolu žili šťastně až do smrti.

KONEC

SPISOVATEL KUBA DÁLEK

Š NIČKA
OU AHOJ SÝKORO DNES SI U NÁS PO DRUHÉ
OJ AHOJ SÝKORO ZASE U NÁS ZA HNÍZDÍŠ ZAS

Michal Šíma:

Byla jednou sýkora, ta hledala partnera. Ale nikde nikdo nebyl. Tak se vydala do města, tam bylo rušno. A lidi se divili co je to za ptáčka? A sýkora fur byla smutnější. Vedle ní sedět samec Jirka. Sýkorka se ptala, jestli nechce být její kamarád? A jednoho dne si sýkorka začala stavět hnízdo.

Figure 44. Outputs of the Birds Online project. An example of products manufactured by children and their teachers from preschools and elementary schools: (a) cotton nestlings with their opened red-yellow bills created according to an original video from a SNBox; (b) a bird nesting created from natural material and paper according to an original video from a SNBox; and (c) birds created from ceramics and knitting wire inspired by birds nesting in a SNBox.

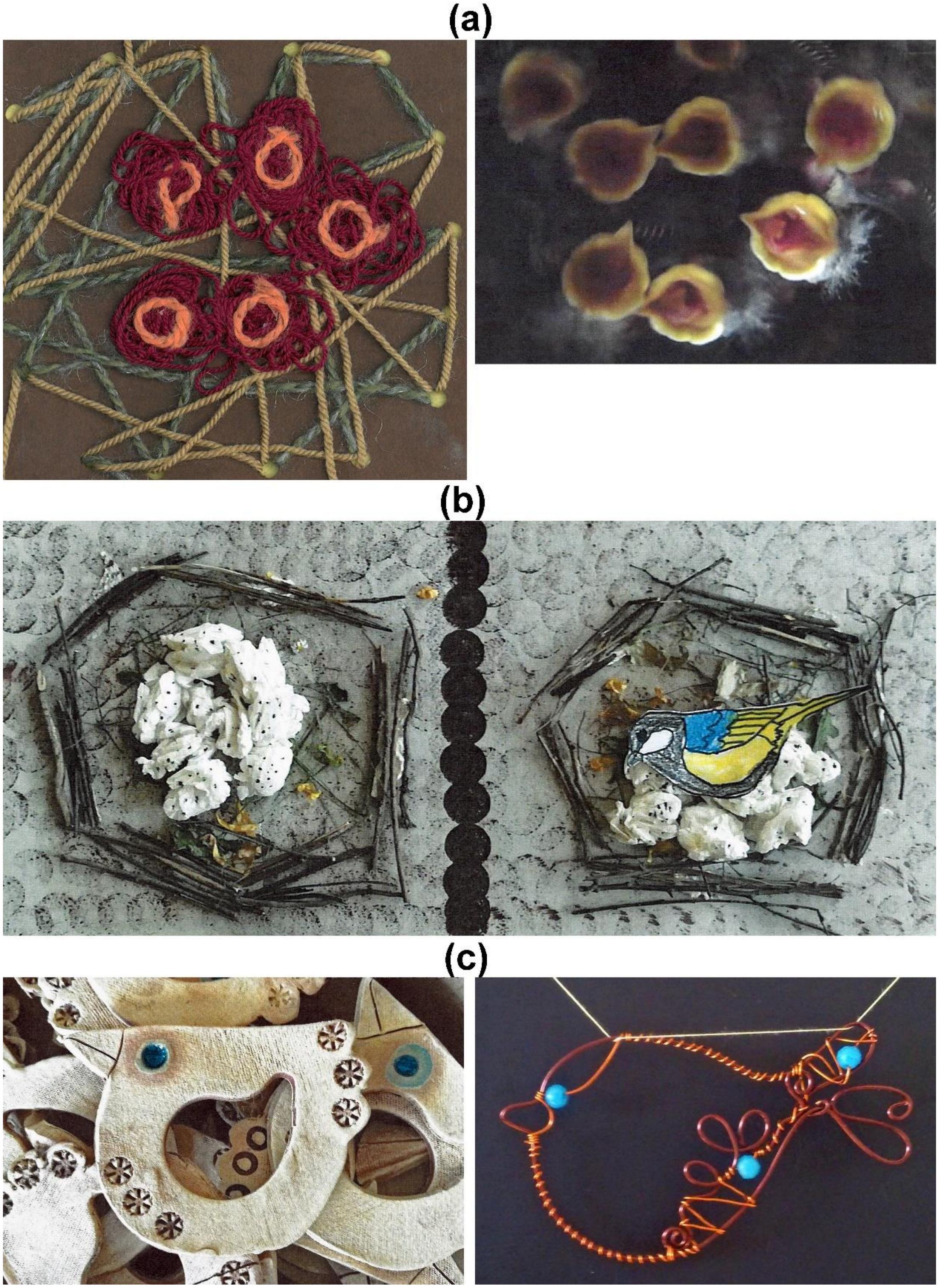
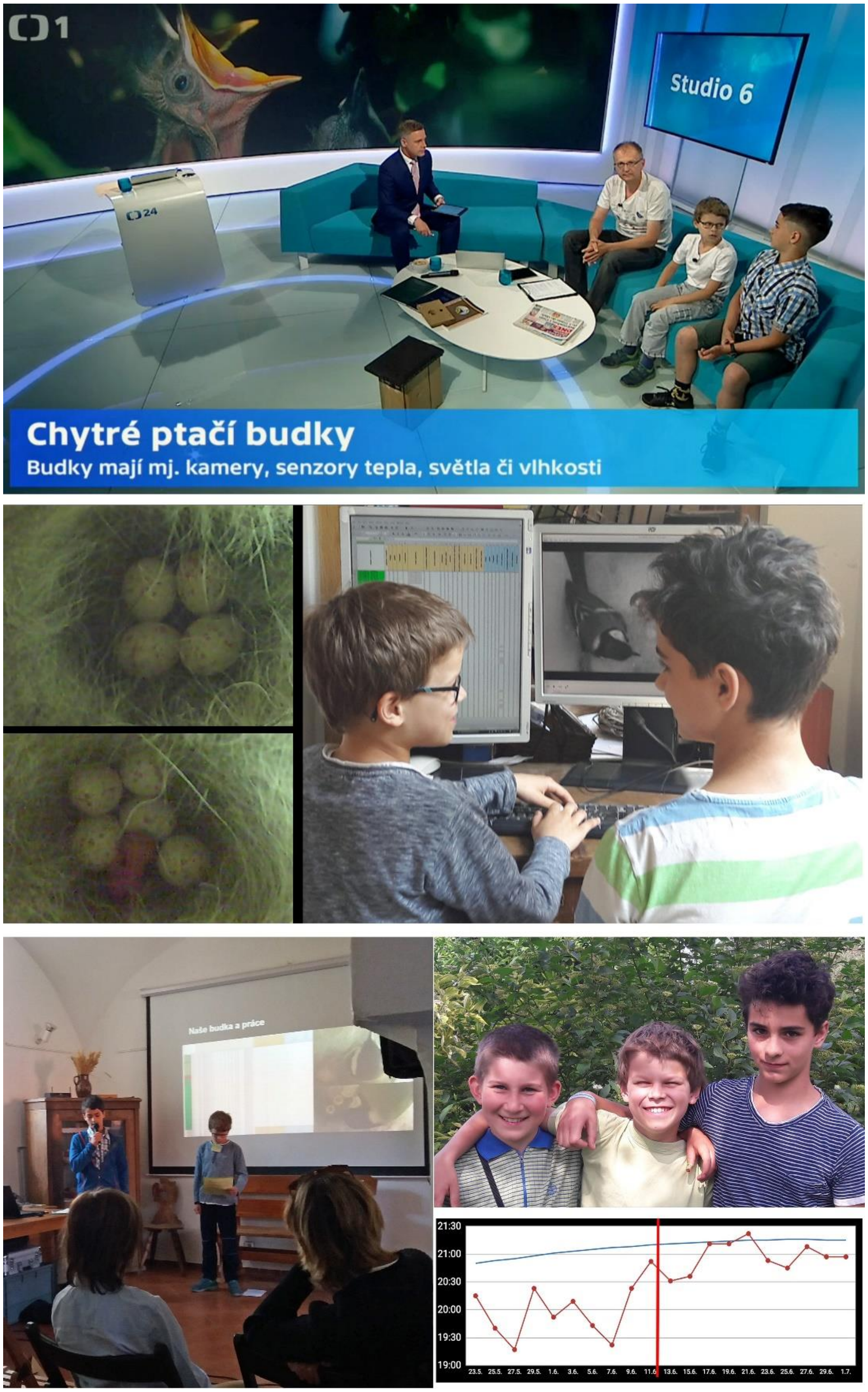


Figure 45. The outputs of the Birds Online project. An example of a presentation created by Patricia Calabria, a teacher from DINO School of Prague, for the purposes of teaching 16–19-year-old students.

Figure 46. The outputs of the Birds Online project. An example of the use of live video streams of nesting birds on computer screens and related desk activities introduced during lessons on the environment and biology in schools with disabled students.

Figure 47. The outputs of the Birds Online project. An example of alternative homeschooling. The boys who analysed the content of video recordings from a SNBox, visualized biological findings, presented the results at the Czech Ornithological Conference for Young People, and introduced their participation in the Birds Online project on Czech television.



4.3 Conclusion

In its design, the Birds Online project has not followed the typical model of Citizen Science projects in several ways. First, the level of automation involved in the collection of data is higher than has typically been the case. With many Citizen Science projects in ecological research, the participants are the sensors (Sullivan et al. 2009). Alternatively, when the collection of data is automated, these data are only often photographs and manual downloads (e.g., Snapshot Serengeti). In contrast, the combinations of video recordings and environmental (contextual) data have been collected and automatically transmitted within our project. Second, the direct engagement of participants in the Birds Online project has been as hosts for SNBoxes, and has required direct interaction of each of these participants with project staff who have installed the SNBoxes. This "partnership" model, which allows for greater sophistication of data collection but at the expense of limiting the number of sites for data collection, has seldom been used (Ryder et al. 2010). Third, we deliberately created opportunities for both informal and formal education, with the formal education being directed to all grades of schools as well as to university students at all levels. As a result — at the level of university education — the more than 1.3 million videos will continue to serve bachelor and master students in creating their theses on biological and methodological (e.g., machine learning) topics, and the large database of unique biological information will serve PhD students and researcher in their studies of life-history strategies in passerine birds and other animals. Additionally, the experience that I have gained from running the Birds Online project will also be reflected in university-level courses (e.g., Citizen Science & Crowdsourcing, Avian Ecology, and Behavioural Ecology).

In retrospect, I think that the Birds Online project was most successful as a demonstration of the technologies that made it possible to automate the collection and dissemination of video recordings for the purpose of public education as well as data that can be used for research. This was only possible because the Birds Online project brought together an interdisciplinary team that included engineers, education specialists, and ecological researchers. In the process of overseeing the Birds Online project, I also came to realize that the most limiting resource for successful Citizen Science projects is the time of project staff to manage and maintain an ongoing project. I mainly paid attention to the number of staff that were required to run Citizen Science projects at the Cornell Lab of Ornithology.

I believe that to shift the Birds Online project from being an experiment and demonstration of technology into a longer-term endeavour will require the creation of more specific research and education objectives, and the hiring of staff whose jobs would be to insure the long-term motivation of the participants, in part through frequent communication to seek feedback from the public.

5 General Outcomes

In this thesis, I have introduced findings that I gained during my 20-year research on ecology and behaviour of Boreal Owls enhanced by the use of new hardware and software tools to automate data collection, and during the 5-year Citizen Science project (called the Birds Online project) applying features found in Internet-of-Thing technology for formal and informal environmental education. The establishment of these projects was only possible due to the interdisciplinary cooperation of ecological researchers, engineers, and education specialists. With the help of engineers, we designed, developed, and applied our own purpose-designed camera system — embedded in a modified wooden nest box and formed the *Smart Nest Box* (*SNBox*) — to collect, manage, and disseminate a diverse array of research and educational data.

Within the *Boreal Owl research*, I used an examination of *the small male hypothesis* in order to demonstrate the benefits gained from the use of our *stand-alone SNBoxes* to monitor Boreal Owl nests located in nest boxes. The video from the SNBoxes allowed me to extract qualitative and quantitative data on provisioning effort of the male owls. I have not found support for the small male hypothesis from these data. While I did identify associations between male size and provisioning behaviour, my findings suggest that the differences in male size represent changes in male mass that reflect the energetic costs to the males experiencing differences in availability of their preferred prey.

More generally, the use of purpose-designed technologies shows how automated data collection can be used to augment the information collected by other means. The data from the SNBoxes are a new addition to a 20-year-dataset on breeding biology and dietary ecology of the Boreal Owl population and 40-year-dataset on monitoring changes in small mammal communities. This long-term research was initiated in our study site in the 1980s by a research group leading by V. Bejček and K. Šťastný in an environment that is far from pristine. Airborne pollutants have led this region to be called the black triangle of Europe. A large proportion of the forest trees are non-native Blue Spruce stands, and restoration is hindered by the high acidity of the soil, harsh mountain weather, and extensive damage to young plantations caused by cervids. The information gained by the SNBoxes provides new insights into how Boreal Owls can live in this environment.

Using the *Birds Online project*, I have demonstrated the use of our *Internet-connected SNBoxes* to monitor nesting birds while engaging people in bird watching, learning about bird life, and participating in the installation and maintenance of SNBoxes. During the 5-year project duration, we have deployed and remotely operated dozens of SNBoxes across the Czech Republic (and also in Poland and the USA) and collected more than 1.3 million videos. To introduce bird watching to the broadest audience, we have cooperated with more than 40 educational institutions. Bird watching available through live streams or video recordings, as well as the installation of SNBoxes at schools' premises, have allowed teachers and their students for various field, digital, and practical educational activities. The development of technologies, the application of SNBoxes in the field, and the use of the project's outputs have also allowed engaging bachelor, master, and PhD students. While I have documented that IoT technologies can effectively serve as a tool for efficient dissemination of environmental education, the transformation of this experimental project to a long-term proficient Citizen Science project will require the creation of more specific research and education objectives, and the hiring of staff whose jobs would be to ensure the long-term motivation of the participants.

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