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Impact of the colonies of great cormorants (*Phalacrocorax carbo sinensis*) on mammals

DOCTORAL DISSERTATION

Natural Science,
Ecology and Environmental Science **N 012**

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VILNIAUS UNIVERSITETAS
GAMTOS TYRIMŲ CENTRAS

Marius
JASIULIONIS

Didžiojo kormorano (*Phalacrocorax carbo sinensis*) kolonijų poveikis žinduoliams

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Gamtos mokslai,
Ekologija ir aplinkotyra **N 012**

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CONTENTS

ABBREVIATIONS

Ad. – adult
BT – breeding time of the cormorants
D – daytime
ECC – great cormorant colony in Elektrėnai
JCC – great cormorant colony in Juodkrantė
Juv. – juvenile
LCC – great cormorant colony in Lukštas
NCC – great cormorant colony in Naudžiūnai
N – night
NT – non-breeding time of the cormorants
Sub. – subadult
T – twilight

INTRODUCTION

Relevance of the study. Small mammals are indicators of forest ecosystem sustainability and play an important role in many other ecosystems worldwide (Carey and Harrington, 2001; Pearce and Venier, 2005; Bogdziewicz and Zwolak, 2014). Being mostly common, small mammals are core components in food webs and have important roles in the functioning of ecosystems (Jedrzejewski and Jedrzejewska, 1992; Malecha and Antczak, 2013; Wilson et al., 2017; Grabham et al., 2019; Gryz and Krauze-Gryz, 2019). The composition of the mammal community and species abundances are not stochastic, they depend from the environment (Carey and Harrington, 2001; Kozakiewicz and Kozakiewicz, 2008). Diversity, abundance, dominance, sex and age structure, and other indicators of the small mammal community are influenced by environmental conditions. Changes in the structure of vegetation, undergrowth, composition of tree crown cover or forest litter affect small mammal communities (Fox, 1995; Bryja et al., 2002; Briani et al., 2004; Čepukienė and Jasiulionis, 2012). Due to their versatile ecological functions, coarse wood debris is particularly important (Carey and Harrington, 2001).

Apart from anthropogenic effects, colonies of great cormorants (*Phalacrocorax carbo*) are probably the fastest and most strong environmental factor in our climatic zone (Kameda et al., 2006; Klimaszyk and Rzymsky, 2016). Cormorants are vector for the transport of nutrients from aquatic to terrestrial ecosystems (Ellis et al., 2006; Otero et al., 2015). Complex environmental effects of great cormorants lead to enormous ecosystem transformation (Klimaszyk and Rzymski, 2016).

Influence of cormorants on fish stocks and the environment in the territory of breeding colonies caused much debate in society. These birds received a lot of attention in the media. Cormorants were considered as possibly the best-studied bird species (Pūtys, 2012). But still, so far there was no study investigating the effects of cormorants on mammals. The research carried out during the preparation of the dissertation will contribute to the assessment of the complex environmental impact of cormorants.

OBJECTIVE AND MAIN TASKS OF THE STUDY

The objective was to evaluate the influence of the colonies of great cormorants (*Phalacrocorax carbo*) on the ecological and biological parameters of small mammal communities and the importance and effects of colonies on carnivores and ungulates.

The following tasks were set to achieve the objective:

1. To investigate the effects of the great cormorant colonies on small mammal community composition, species diversity, abundance, demographic structure, body condition and skull morphometry parameters, and to determine if these parameters depend from the size of the cormorant colony.
2. To evaluate the influence of cormorant-transmitted nutrients on the isotopic niche of small mammals using stable isotope analysis.
3. To analyze the accumulation of chemical elements in the tissues of small mammals under the colonies of great cormorants.
4. To determine the impact of cormorants colonies on seasonal and daily activities of carnivores and ungulate mammals.

STATEMENTS TO BE DEFENDED

1. Diversity and abundance of small mammal communities, sex and age structure, body condition and skull morphometry were changed under the influence of cormorant colonies.
2. The initial positive effects of cormorant colonies on the ecological and biological parameters of small mammals are changed to negative when colony reaches the certain size.
3. Nutrients, transported by cormorants from the aquatic to the terrestrial ecosystems are influencing the nutrient balance and shifting isotopic niche of small mammals.
4. Expansion of the great cormorant colony immediately increases the input of biogens to the terrestrial ecosystem, and this influence is reflected by increased nitrogen stable isotope values in the hairs of small mammals.
5. Although the effects of cormorant colonies are not so strong as those of anthropogenic pollution sources, they affect the concentrations of K, Cu, Rb, and Pb in the tissues of small mammals.
6. Cormorant colonies are important habitats for some ungulates and carnivores, where bird activity affects seasonal and daily activity patterns of some species.

NOVELTY OF THE STUDY

In this work the effects of great cormorants on mammals were scientifically evaluated for the first time. The study revealed the effect of cormorant colonies on the diversity and abundance of small mammal communities, sex and age structure of their populations and the body condition of individuals. We found, that the initial positive effects of cormorant colonies on the ecological and biological parameters of small mammals are changed to negative when colony size reached a certain level. The influence of a biggest colony of great cormorants on the skull morphometry in two small mammal species was revealed for the first time. Also, for the first time, the influence of cormorants on the accumulation of heavy metals and other chemical elements in mammalian tissues was evaluated, and a stable isotope ratio analysis of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) was performed. The fundamental novelty of our investigation was in evaluating the immediacy of the impact of the great cormorant colony on small mammals. The results for the first time showed how fast biogenic pollution is transferred and what its consequences are to small mammal ecology. We also observed changes in seasonal and daily activity patterns of mammals in the colonies of cormorants during bird breeding time.

The study results provide a better understanding of the long-term effects of great cormorants on the ecosystem. Results of this research are important both for assessing the effects of cormorant colonies on mammals and for understanding the evolution of mammalian population parameters in an extremely rapidly changing environment. Our investigation contributes to understanding biological pollution and disturbance through the complex environmental changes occurring in cormorant colonies.

1. LITERATURE OVERVIEW

1.1. Distribution and biology of great cormorants (*Phalacrocorax carbo*)

Phalacrocoracidae is a bird family with approximately 40 species of aquatic birds breeding in colonies. The great cormorant (*Phalacrocorax carbo*) is the most widespread member of this family, found nearly everywhere in the world: Africa, Australia, most of Eurasia and North America on the northern Atlantic coast (Hoyo et al., 1992). Two subspecies of great cormorants *Phalacrocorax carbo* breed in Europe: *P. c. carbo* and *P. c. sinensis.* The „Atlantic“ subspecies *P. c. carbo* breeds in France, United Kingdom, Ireland and Norway. Nests are mainly found in islands on exposed marine coasts or rocky cliffs. The „Continental” subspecies *P. c. sinensis* breeds in continental Europe, Scandinavia and along the coasts of the Baltic Sea. Nests are mainly found in trees and on land near shallow coasts (Bregnballe et al., 2011).

The breeding of cormorants in Lithuania begins in March. They lay 2–4 eggs, which hatch after 27–31 days. The chicks leave the nest at 2 months of age but return to the nest for more than a month to be fed of their parents (Nelson, 2005; Knyva and Rumbutis, 2016). So, in the breeding colonies, cormorants are huddled from early March to late July.

Cormorants are specialized ichthyophages. Roach, perch and ruff are the major part, 70%, of the diet, and almost 78% of it consists of fish under 12.5 cm in length (Pūtys, 2012). Prey is catched by diving. The chicks are fed by cud fish from the stomach. Some of the fish brought into the colony to feed chicks are lost. Daily food requirement for adult bird is about 240 g of fish per day. When feeding juveniles, one cormorant must catch between 300 g and almost 600 g of fish per day (Gremillet et al., 1995).

1.2. Dynamics of abundance of great cormorants

Due to persecution (hunting, destruction of breeding colonies), the continental subspecies of cormorants (*P. c. sinensis*) was extinct in almost all of Europe in the 20th century. As a top predator, populations of cormorants have been affected by the use of DDT and polychlorinated biphenyl (PCB). In the 1970s, cormorants colonies were only left in the Netherlands, Germany, Sweden and Poland. The number of breeding pairs at that time was only 3500–4300 (Bregnballe, 1996). Later, the cormorant population began to increase. Population growth was 10–20% yearly. In 1995 it was estimated more than 130,000 of breeding pairs (Eerden and Gregersen, 1995; Steffens, 2010; Bregnballe et al., 2011; Kohl, 2015). Ten years later, in 2005 the number of breeding cormorant pairs in Europe doubled and reached 240,000 (Fig. 1). In 2014 number of breeding pairs of *P. c. sinensis* was estimated at 256,000. In addition to these, 42,000 pairs of *P. c. carbo* were breeding in Europe (Kohl, 2015). Thus, the abundance of the European cormorant population over the last decade has stabilized. The recovery of cormorant populations was driven by increased breeding success and survival once the requirements of the EU Birds Directive have been implemented. Directive ensured the protection of breeding colonies and protection against shooting (Lindell et al., 1995; Steffens, 2010). Also, fast increase of the cormorant numbers was related to high prey availability: development of large, shallow, and very fertile aquaculture fish farms areas in addition to the eutrophication of other water bodies (White et al., 2011; Herrmann, 2019).

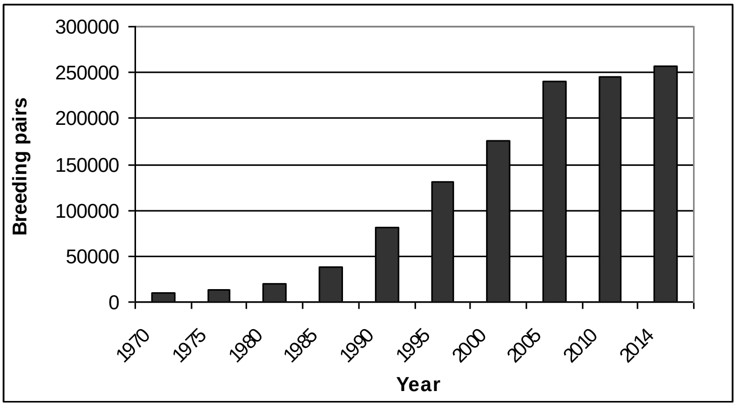

Fig. 1. Development of *P. c. sinensis* breeding population (pairs) in Europe (excluding Ukraine and Moldova) (according Kohl, 2015, modified).

1.3. Environmental impact of the colonies of great cormorants

Like other piscivorous colonial breeding birds, great cormorants are ecosystem engineers (Jones et al., 1994; Ayers et al., 2015), able modulate the availability of resource to other species and extremely change the ecosystem in the territory of the breeding colony (Klimaszyk and Rzymsky, 2016). Due to dense nesting, numerous nesting birds and large areas of the breeding colonies, cormorants are birds that have huge effects on their breeding area (Kameda et al., 2006). The number of breeding pairs in the largest colony in Lithuania overruns 3,000. There are several times bigger colonies in Europe, for example, the number of breeding pairs in the cormorant colony located at Katy Rybackie (Poland) exceeds 11,000 (Misztal-Szkudlinska et al., 2011). Cormorants are effective vector for the transport of nutrients from aquatic to terrestrial ecosystems (Ellis et al., 2006; Otero et al., 2015) and thereby affect the nutrient status of the soil (Ishida, 1996; Hobara et al., 2001). Territories of the cormorant colonies are overloaded with extremely high concentrations of phosphorus (P) and nitrogen (N) as a result of deposited faecal material, lost regurgitated fish and dead chicks (Kuiken et al., 1999; Gwiazda et al., 2010; Garcia et al., 2011; Klimaszyk and Rzymski, 2016). The effect is stronger near cormorant nests (Kolb et al., 2015). A single bird deposits 20–50 g of faeces per day. Great cormorants spent about 20 h daily in the breeding colonies, so about 80% of faeces are deposited there (Klimaszyk and Rzymsky, 2016). Cormorant faeces contain about 10% of N and 8% of P (Gwiazda et al., 2010). Deposited faeces overload the ecosystem with N and P by 10^4 to 10^5 times (Garcia et al., 2011). As was shown by Klimaszyk et al. (2014, 2015), soils beneath the colony contained extremely high concentrations of nitrogen and phosphorus. Soil within cormorants breeding colonies was more acidic and had a higher concentration of K (Lafferty et al., 2016). In addition, cormorants and other colonial birds produce a large amount of ammonia (NH_3) (Riddick et al., 2012). Topsoil in the great cormorant colonies was characterized as geochemical anomalies with prevalence of S, Cu, P, Cl, Ti, Ca, Cr, Zn, Ni, Pb and Sb (Taraškevičius et al., 2013).

Complex environmental effects of great cormorants can lead to enormous ecosystem transformation (Klimaszyk and Rzymski, 2016). Chemical properties of soil induce changes of the forest ecosystem and plants (Anderson and Polis, 1999; Kameda et al., 2006). Seabird colonization increases N and P levels and affect plants from a few (Hobara et al., 2005) to 10 years (Veum et al., 2019) or even 20–60 years after colony abandonment (Ishizuka, 1966; Kameda et al., 2006). Bird-induced chemical loadings negatively affect tree health (Lafferty et al., 2016). Moreover, canopy cover in bird colony is reduced (Veum et al., 2019) as well as tree seedling diversity (Maesako, 1999). Ishida (1996) suggest that forests structure and tree species composition in cormorant colonies is simplified. Investigation in the colony of great cormorants in old-growth pine forest (Juodkrantė, Lithuania) showed that numbers of the plant species, as well as the coverage of vegetation, varied depending on the cormorant influence level (Matulevičiūtė et al., 2018). Significant vegetation changes occurred in several years after colony settlement. In 10 years pine forest ecosystem became destroyed: all trees in the territory were dead, characteristic plant species of the coniferous forest ecosystem disappeared (Matulevičiūtė et al., 2018).

Impact of great cormorants on the forest resulted changes in species richness of myxomycetes; smallest number of species was found in the most active part of the colony (Adamonytė et al., 2012). It is known, that species composition and number of lichens was significantly modified in the birds colonies (Zolkos et al., 2013). Lowest numbers of the lichen species were found in the part of the Juodkrantė cormorant colony with the highest nest density (Motiejūnaitė et al., 2014). Furthermore, in cormorant-disturbed forest changes in the structure of fungal communities were observed: decrease of mycorrhizal species, the presence of coprophilous fungi on forest litter, and the appearance of host-specialized fungi on plants (Kutorga et al., 2013).

In response to the influence of nesting cormorants, soil microbial community and soil and litter fauna structure was transformed (Kolb et al., 2015). With increased intensity of avian incluence bacterial diversity decreased (Domínguez et al., 2016). Dominance of plant feeders in the arthropod community at cormorant colony shifted to dominance of carrion and dung feeders. Larger impacts on arthropods were observed in the area with longer existence of colonies (Craig et. al., 2012). Insect, spider and lizard abundances were significantly higher on islands affected by bird colonies (Polis and Hurd, 1996). Seabird colony had positive effects on distribution and body condition of herpetofauna (Kohno and Ota, 1991).

However, amongst the studies analyzing effects of ornithogenic impact on environment, there have been no investigations on the cormorant colony impact on mammals. The only exception was preliminary notice that foxes (*Vulpes vulpes*), racoon dogs (*Nyctereutes procyonoides*) and wild boars *(Sus scrofa*) were often observed visiting the colony in Katy Rybackie (Poland) (Goc et al., 2005).

1.4. Cormorant colonies in Lithuania

In Lithuania great cormorants usually breed in mixed colonies with grey herons. Colonies are mostly established near the shores of a water bodies. Cormorants choose tall trees for nesting (Knyva and Rumbutis, 2016). In Lithuania cormorant breeding on the ground was not observed.

Majority of nests are located in pines, some nests were observed in spruce, black alder and birch trees (Dagys and Zarankaitė, 2013). Most of the nests in the cormorant colony in Juodkrantė are twisted in pines, occasionally in spruce and oak trees. In the cormorant colony in Lukštas most nests are twisted in black alder, pine and birch trees. In colonies of Elektrėnai and Naudžiūnai nests are twisted in pines. In recent years, cormorant nests have been observed in oaks as well. In 2012, Lithuania had six colonies of great cormorants with 3200 occupied nests (Dagys and Zarankaitė, 2013). In 2016 Lithuania had seven cormorant colonies with about 5600 occupied nests (Knyva and Rumbutis, 2016). The largest cormorant colony is located on the Curonian Spit near Juodkrantė, and in different years it contained from 60–80% of the national breeding population (Knyva and Rumbutis, 2016). This colony has been known since 1803. However, due to constant persecution, the Juodkrantė colony was abandoned by the cormorants in 1887 (Gražulevičius and Elertas, 2005). After more than 100 years of eradication, great cormorants started to breed again there in 1989 (Stanevičius and Paltanavičius, 1997). The colony was growing rapidly, crossing the threshold of 500 nests in 1995, 1000 nests in 1999, and 2000 nests in 2003. In 2011–2016 number of breeding pairs in this largest colony in Lithuania was between 3800 (2015) and 4941 (2013). During the activities on abundance regulation, from 9.5% (2011) to 64% (2012) of eggs in the nests were cooled, with the total of 34% of eggs cooled during this period. In 2015 cormorant abundance was not regulated (Knyva and Rumbutis, 2016). From 2017 to 2019, the abundance of cormorants in the Juodkrantė cormorant colony was very stable (about 3000 breeding pairs). During this period, 50% of the juveniles in the nests did not hatch due to the regulation of cormorant abundance (S. Rumbutis pers. com.).

2. STUDY SITES

The investigation was done in 4 colonies of the great cormorants located in Lithuania (Table 1, Fig. 2). The territory and surroundings of the great cormorant colony in Juodkrantė (further **JCC**) according to duration and degree of colony impact on the environment was divided into five zones (**Paper I**, Fig.1; **Paper VI**, Fig. 1):

- the ***control zone*** **(I)** with no influence of cormorants on the habitat.
- the ***zone of initial influence*** **(II)** is expanding part of the colony, with the most recent and still developing influence. In this zone, trees are still alive, but with reduced vitality, shrub layer reduced and herb layer is scarce. Moss layer is thin, with bare patches.
- the ***zone of long-term influence*** **(III)** of the colony with the highest concentration of nests. Trees are dead or dying and the shrub layer is reduced, the projection cover of the herb layer is 10% or less.
- the ***zone of former active influence*** **(IV)** of the colony with dead trees, many of them rotten, fallen and decaying. The territory is re-growing with young trees and shrubs, the herbaceous layer is thick. This is abandoned part of the colony with only a few nests still in use.
- the ***zone of the ecotone*** (**V**), situated between influenced zones and surrounding forest (more details in **Paper I**).

In the cormorant colonies at Lukštas (further **LCC**), Naudžiūnai (**NCC**) and Elektrėnai (**ECC**) only two zones were defined: those with colony influence (***colony*** (**II-V**)) and with no influence on the habitat (***control*** (**I**)). Distance between colonies and controls ranged from 50 m (Elektrėnai) to 200 m (Lukštas).

Table 1. Main characteristics of investigated colonies in the study period.

Colony and location	**LKS coordinates**	**Predominant tree species**	**Area, ha**	**Breeding pairs of great cormorants* (grey herons)**
Juodkrantė shore of the Curonian Lagoon	317462, 6157742	pine, spruce, birch, oak	14	1500–3800 (230–340)
Lukštas peninsula of the Lukštas Lake	637836, 6192828	black alder, pine, birch	1	90–130 (0)
Naudžiūnai shore of the Nemunas River	499837, 6050225	pine, spruce	0.3	80 (40)
Elektrėnai island of the Elektrėnai Lagoon	543661, 6069593	pine, birch, oak	1.5	120–160 (40–90)

*– after the regulation of abundance

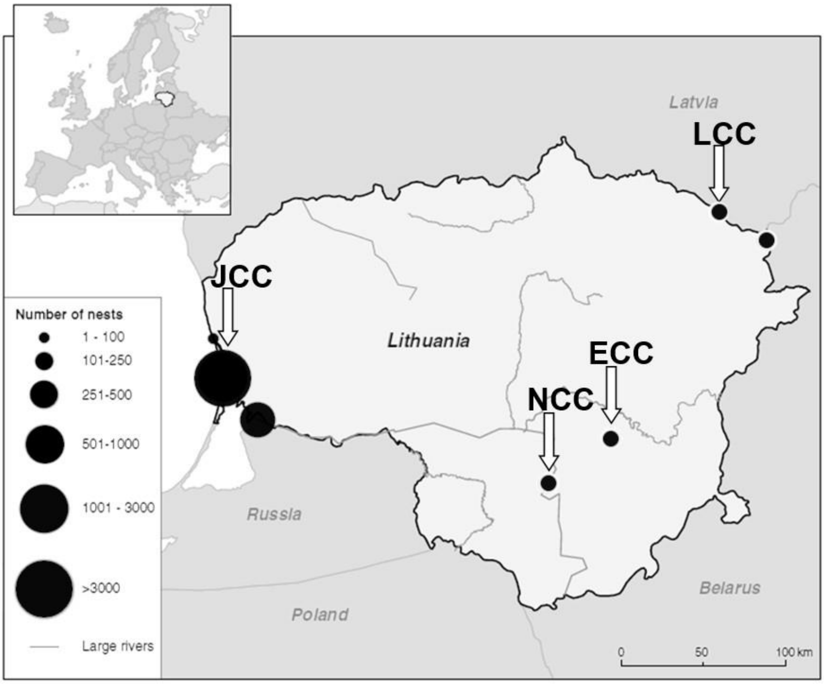

Fig. 2. Investigation sites (cormorant colonies marked by dots, investigated colonies marked by arrows): **JCC** – Juodkrantė cormorant colony, **NCC** – Naudžiūnai cormorant colony, **ECC**– Elektrėnai cormorant colony, **LCC** – Lukštas cormorant colony (map according Dagys and Zarankaitė, 2013).

3. MATERIALS AND METHODS

3.1. Impact of cormorants on ecological and biological parameters of small mammals

Small mammal trapping was done by snap trap lines, each consisting of 25 traps spaced 5 m from each other. Dried brown bread soaked in sunflower oil was used as a bait. In all years trapping was done from September to November; additional trapping in June 2013 and 2014 was conducted in Juodkrantė cormorant colony. Traps were exposed for 1–3 days and checked once a day (Balčiauskas, 2004). Totally, in 4 cormorant colonies 257 snap trap lines were operated in 2011–2019, with a total sampling effort of 17700 trap days (Table 2). Trapped small mammals were identified, weighed (with accuracy of 0.1 g) and measured (with accuracy of 0.1 mm). Individuals were then dissected, age and sex identified. Three age categories were used, based on the presence and involution of the thymus gland and reproductive status of the animals (**Paper II**). The relative abundance of small mammals was expressed as the number of individuals per 100 trap days, based on the number of individuals trapped in the first day. We used Shannon's diversity index H (log base 2), Simpson's dominance index c (according to Krebs, 1999). We used the body condition index $bc=(Q/L^3)\times10^5$, where Q is body weight in g and L is the body length in mm (Moors, 1985). The number of embryos and the number of fresh placental scars were counted to determine litter size (Balčiauskas et al., 2012).

3.2. Skull morphometry

Skull morphometry was analyzed in 468 yellow-necked mice (*Apodemus flavicollis*) and 151 bank voles (*Myodes glareolus*) individuals, trapped in Juodkrantė colony. Under a binocular microscope with a micrometric eyepiece which has an accuracy of 0.1 mm, 23 skull characters were measured (list of measured characters presented in **Paper III**). We tested if differences in the size of skull characters were present and, if so, whether these differences were associated with possible drivers of change – i.e., zone of the colony, trapping year, trapping month, animal age and animal sex (**Paper III**).

Table 2. Trapping effort, trap days in the colonies of the great cormorants in Lithuania, 2011–2019. Number of trap lines presented in the brackets.

	Cormorant colony			
Year	**Juodkrantė**	**Lukštas**	**Naudžiūnai**	**Elektrėnai**
2011	750 (15)	–	–	–
2012	2225 (31)	–	–	–
2013	2400 (35)	–	–	–
2014	2175 (30)	600 (8)	–	200 (8)
2015	750 (10)	600 (8)	–	600 (8)
2016	750 (10)	200 (8)	600 (8)	–
2017	750 (10)	600 (8)	600 (8)	–
2018	750 (10)	600 (8)	600 (8)	–
2019	750 (10)	600 (8)	600 (8)	–
Total:	***11300 (161)***	***3200 (48)***	***2400 (32)***	***800 (16)***

3.3. Stable isotope analysis

Two species of small mammals, *A. flavicollis* and *M. glareolus* were used for stable isotope analysis. Small mammals were trapped in Juodkrantė, Elektrėnai and Lukštas cormorant colonies. All three colonies had control zones. In addition, small mammals were also trapped in control site with no breeding cormorants at Zarasai (**Papers IV, V**) and Rusnė (**Paper VII**). Altogether, hair samples were taken from 129 individuals of *A. flavicollis* and from 120 individuals of *M. glareolus* (**Papers IV, V, VII**). Isotopic signatures were evaluated and isotopic baselines were established from possible dietary items (**Paper V)**.

Small mammals hair samples were clipped off between the shoulders of specimens, each sample placed separate and stored dry in bags. Prior to the stable isotope analysis hair samples were scissored off, weighed with a microbalance and packed in tin capsules (Paper IV, V, VII). Environmental samples (including plants, litter, invertebrates) were stored in different bags in refrigerator under -20 °C prior to preparation and analysis. Samples were oven dried in 60 °C to a constant weight for 24–48 hours then homogenized to a fine powder by mortar and pestle and Retsch mixer mill MM 400 (Paper V).

Stable isotope ratios (expressed as $\delta^{13}C$ and $\delta^{15}N$) were measured using elemental analyzer (EA) coupled to an IRMS (Flash EA1112; Thermo Delta V Advantage, Thermo Scientific, USA). Stable isotope data are reported as δ values, according to formula:

$$\delta X=(R_{sample}/R_{standard}-1)*10^3,$$

where $R_{sample}={}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$ of sample, $R_{standard}={}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$ of standard **(Paper IV, V, VII)**.

3.4. Study of chemical elements

Chemical elements were analyzed in 54 individuals (23 males, 31 females; 21 adults, 21 subadults and 12 juveniles) of the dominant species *A. flavicollis* captured in Juodkrantė cormorant colony and control zone. We used the body (muscle and bones) samples to register the presence and concentration of the following 20 elements: Na, Mg, Al, Si, P, S, Cl, K, Ca, V, Mn, Fe, Ni, Cu, Zn, Br, Rb, Sr, Mo and Pb. The sampling unit used was skinned body of one individual without internal organs. Samples were oven dried at 100 °C for 12 h, crushed in agate mortars and later pre-mineralized to dry ash at 240 °C. Ashed samples were milled using the MM 400 mill with zirconium oxide grinding jars and grinding balls. Milled samples were mixed with the Licowax binder (Fluxana) in the proportions of 1.25 g of material and 0.28 g of binder (dilution factor 0.816, as recommended by the equipment manufacturers). Each sample was homogenized and pressed for 3 min using 15 KN (press PP25) to produce 20 mm diameter pellets. The pellets were analyzed by energy-dispersive xray fluorescence (EDXRF) equipment Xepos HE (Kleve, Germany) using TurboQuant (TQ) II for pellets calibration module as elaborated by the manufacturers. Concentrations of chemical elements were expressed on a wet weight basis in mg g^{-1} (**Paper VI**).

3.5. Camera trapping

The activities of mammals were evaluated using camera traps (system with a motion trigger/sensor that activates a camera to take a photograph when an animal is present). We deployed camera traps in three points (one camera per point) in the **JCC** and one point in **LCC**.

Camera trapping in **JCC** lasted from November 2014 to September 2015 and from June 2017 to October 2018 involving 1376 trap days of effort. Camera trapping in **LCC** lasted from February 2015 to February 2016 and from November 2016 to July 2019 involving 1317 trap days of effort.

We used Ltl Acorn-5210A cameras with sensors were set to the maximum sensitivity and trigger interval set at 0 sec. We used trail-targeted (passive camera) trapping design with no attractants. Cameras were mounted on the trees about 40–60 cm above ground and checked (replacing batteries and SD memory cards) 3–4 times during the year. Time and date were automatically recorded on each picture. Pictures taken with at least 1-hour interval were treated as independent observations (trap events). Camera day lasted from 00:00 to 23:59. Year was divided into periods of the cormorant breeding time (BT) and non-breeding time (NT). BT lasted from April (when chicks begin to hatch from eggs) to July (when chicks finally leave the cormorant area). Non-breeding time was the period from August to March.

Each day was divided into three periods: daytime, nighttime and twilight. Twilight (T) was defined as a 60 minutes period before and after sunrise/sunset, so that each day had four twilight hours. Daytime (D) was a period between 60 minutes after sunrise and 60 minutes before sunset. Night (N) was a period between 60 minutes after sunset and 60 minutes before sunrise. Time of sunset and sunrise were estimated using the website www.day.lt (**Paper VIII**).

3.6. Statistical analysis

STATISTICA for Windows, ver. 6.0 software (StatSoft 2004) was used for the statistical analyses (**Paper I–VIII**). Multifactor influence was tested using main effects ANOVA for all skull measurements and potential predictor (zone of the colony, trapping year, animal age and sex) (**Paper III**). The $\delta^{15}N$ and $\delta^{13}C$ values in the samples were expressed as arithmetic mean±SE (standard error) (**Paper IV, V, VII**). A main effect ANOVA was used to test the influence of the species, site, territory (colony and control), animal gender and age on carbon and nitrogen stable isotope values, with Wilk's lambda to test the significance of influence. The post-hoc Tukey test was used for comparing multiple independent groups (**Paper IV)**. The normality of the distribution $\delta^{15}N$ and $\delta^{13}C$ values was evaluated using Kolmogorov-Smirnov test. As not all values of $\delta^{15}N$ and $\delta^{13}C$ were distributed normally, the influences of species and the zone of the colony on the carbon and nitrogen stable isotope values in the mammal hair were tested using nonparametric Kruskal-Wallis ANOVA (**Paper V, VII**). In study of chemical elements the influences of multifactors were tested using MANOVA. The influences of zone, gender and age were tested using two-way ANOVA with Wilk's lambda for significance. The Tukey post-hoc test was used to compare multiple independent groups **(Paper VI).** Relative shooting frequency **s**ignificance of differences was evaluated using ANOVA, pairwise comparisons according Student’s t. Daily activity patterns were compared using chi-square statistics (**Paper VIII**).

4. RESULTS AND DISCUSSION

Detailed results and the discussions on data were published and are available in papers (**Papers I–VIII**). Below are the summaries of the dissertation results and discussion covering this study.

4.1. Impact of cormorants on ecological and biological parameters of small mammals

During nine-year study (Table 2) 1967 individuals of 10 small mammal species were trapped in the 4 colonies of the great cormorants and in their control territories (Tables 3–5): common shrew (*Sorex araneus*), pygmy shrew (*S. minutus*), water shrew (*Neomys fodiens*), *M. glareolus*, meadow vole (*Microtus agrestis*), root vole (*Microtus oeconomus*), house mouse (*Mus musculus*), harvest mouse (*Micromys minutus*), striped field mouse (*Apodemus agrarius*) and *A. flavicollis*.

The dominant species in **JCC** was *A. flavicollis*, accounting for 70.6% of all trapped individuals (Table 3). *A. flavicollis* dominated in all **JCC** zones comprising from 65.0% (in zone IV) to 94.0% (zone II) of the small mammal community. *M. glareolus* was subdominant in all zones (Table 3). Six small mammal species were recorded in the control zone (I) and five species in the ecotone (V). In the most active part of the colony, i.e., zone of initial influence (II) and zone of long-term influence (III) small mammal species richness was poor, 3 and 4 species respectively. The highest number, 7 species was found in the zone of former influence of the colony with abandoned nests.

The lowest ***relative abundance*** of small mammals in **JCC** was found in the zones II and III, 4.65±1.08 and 4.76±1.41 ind./100 trap days (±SE), respectively. The highest abundance was registered in zones V and IV, 20.96±2.82 and 22.46±1.85 ind./100 trap days (Fig. 3). Relative small mammal abundance in control zone (10.38±1.51) was significantly lower than in zones V ($t=3.49$, $p<0.001$) and IV ($t=5.04$, $p<0.001$), while significantly higher than in most affected zones II ($t=3.04$, $p<0.01$) and III ($t=2.72$, $p<0.01$). Also, relative abundance in zones IV and V was significantly higher than in zones II and III (all $p<0.001$).

Extremely low small mammal ***species diversity*** was observed in zone II (Shannon's H=0.37). The highest species diversity was found in zone IV (H=1.33) (Table 3). Dominance was highest in zone II (Simpson's c=0.89). In other zones, Simpson's index was relatively stable (c=0.56–0.63).

In the control zone of **LCC** dominant species was *M. glareolus* (58.4%), with *A. flavicollis* being subdominant (30.5%). *M. glareolus* was dominant in the colony (66.9%) also. The subdominant species in the cormorant affected zone was *A. agrarius*, comprising 18.1% of the trapped small mammals. The area affected by cormorants exhibited greater species richness (9 species) than control zone (6 species), although diversity indexes did not differ significantly (Table 4). Relative abundance was 2 times higher in the colony (29.17±2.92 ind./100 trap days) compared with control (13.50±2.14) ($t=4.33$, $p<0.001$).

Only two small mammal species were trapped in the control of **NCC**, *A. flavicollis* comprising 57.4% and *M. glareolus*, 42.6% of all trapped individuals. Species richness was higher in the colony: five species with dominants *M. glareolus* (45.4%) and *A. flavicollis* (41.2%) and subdominant *A. agrarius* (11.9%). Species diversity was higher in the colony (Shannon's H=1.52) than in control (H=0.98). Dominance was higher in the control (c=0.51). Small mammal abundance in the colony was two times higher than in control zone (Table 5) ($t=3.13$, $p<0.01$).

Only one species, *M. glareolus*, was found in colony (21 ind.) and control zone (24 ind.) of **ECC**. Relative abundance was almost identical, 7.00±2.36 and 8.00±2.73 ind./100 trap days, respectively ($t=0.28$, $p=0.79$).

Paper I represents an initial investigation into the loss of diversity in a small mammal community in JCC.

The ***sex and age structure*** of *A. flavicollis* trapped in **JCC** was evaluated between zones (Fig. 4). Sex ratios in control and ecotone were identical (males 48.9%, females 51.1% in both). In the zones with cormorant influence males prevailed, though not always significantly: 54.5% in zone IV (as in control, $\chi2=1.26$, $p=0.26$), 55.8% in zone II (as in control, $\chi2=1.91$, $p=0.17$) and 68.3% in zone III (more than in control, $\chi2=15.1$, $p<0.01$). Only in zone III difference from 1:1 sex ratio was significant ($\chi2=13.4$, $p<0.001$).

Sex ratios of adult *A. flavicollis* in **JCC** was similar in control zone (males 56.9%, females 43.1%), zone V (males 57.5%, females 42.5%) and zone IV (males 58.4%, females 41.6%). In the zones most affected by cormorants (II and III) the proportion of males was 68.4% in zone II (more than in control, $\chi2=5.45$, $p<0.05$) and 66.7% in zone III (more than in control, $\chi2=3.92$, $p<0.05$). Greater proportion of females was observed in immature (juvenile and subadult) *A. flavicollis* in control zone of **JCC** (males 43.9%, females 56.1%) and ecotone (males 41.4%, females 58.6%).

Males prevailed also in the other zones, but not necessarily significantly: 51.7% in zone II (as in control, χ2=2.48, p=0.12), 69.2% in zone III (more than in control, χ2=26.1, p<0.01) and 51.9% in zone IV (as in control, χ2=2.63, p=0.11).

The age structure of *A. flavicollis* in **JCC** also differed between zones: the greatest proportion of juveniles (40.3%) and the smallest proportion of adults (24.7%) was found in zone II (χ2=8.84, p<0.05). The smallest proportion of juveniles (20.4%) and the greatest proportion of adults (46.8%) was characteristic to ecotone (V) (compared to control zone χ2=10.74, p<0.001). The proportion of subadults in different zones was similar: from 25.6% in control to 35.0% in zone II.

Table 3. Small mammal community structure, diversity and relative abundance (RA, ind./100 trap days) in the zones of different influence of the great cormorant colony in Juodkrantė, 2011–2019. Zones: I – control, II – initial influence, III – long-term influence, IV – former active influence, V – ecotone.

	Zones of the colony					
Species	**I**	**V**	**II**	**III**	**IV**	**Total, n (%)**
S. araneus	2	3	1	0	16	22 (1.9)
S. minutus	2	0	0	0	1	3 (0.3)
My. glareolus	38	91	4	17	135	285 (24.8)
M. agrestis	0	1	0	1	4	6 (0.5)
M. oeconomus	1	2	0	1	6	10 (0.9)
M. minutus	3	0	0	0	8	11 (1.0)
A. flavicollis	142	210	79	63	316	810 (70.6)
Total	**188**	**307**	**84**	**82**	**486**	**1147**
Shannon's H	1.047	1.034	0.369	0.918	1.33	1.149
Simpson's c	0.612	0.556	0.887	0.634	0.502	0.561
RA±SE	10.38±1.51	20.96±2.82	4.65±1.08	4.76±1.41	22.46±1.85	12.54±0.99

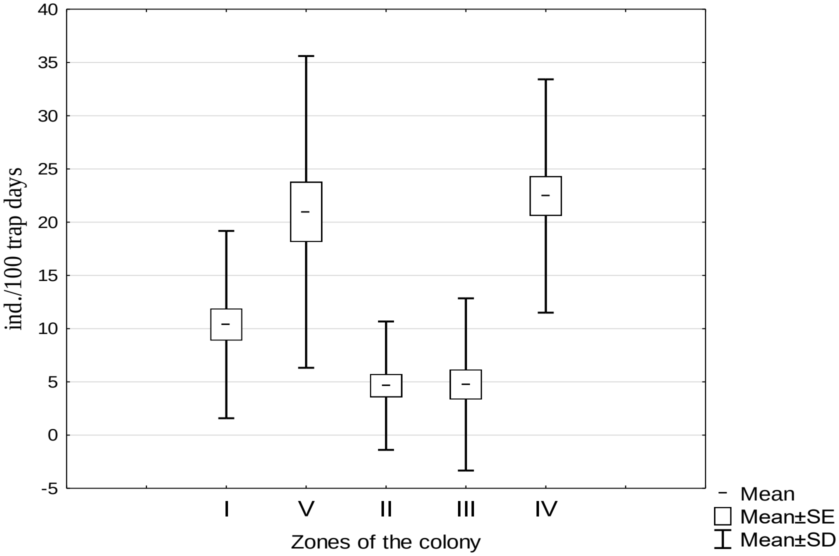

Fig. 3. The relative abundance (RA) of small mammals in different zones of the great cormorant colony in Juodkrantė. Zones: I – control, II – initial influence, III – long-term influence, IV – former active influence, V – ecotone.

Table 4. Small mammal community structure, diversity and relative abundance (RA, ind./100 trap days) in the control zone (**I**) and the colony (**II-V**) of the great cormorants in Lukštas, 2014–2019.

Species	**I**	**II-V**	**Total, n (%)**
S. araneus	7	18	25 (4.9%)
S. minutus	0	2	2 (0.4%)
N. fodiens	0	1	1 (0.2%)
M. glareolus	90	240	330 (64.3%)
M. agrestis	2	5	7 (1.4%)
M. musculus	0	1	1 (0.2%)
M. minutus	1	1	2 (0.4%)
A. agrarius	7	65	72 (14.0%)
A. flavicollis	47	26	73(14.2%)
Total	**154**	**359**	**513**
Shannon's H	1.509	1.524	1.602
Simpson's c	0.439	0.488	0.456
RA±SE	13.50±2.14	29.17±2.92	21.33±2.12

Table 5. Small mammal community structure, diversity and relative abundance (RA, ind./100 trap days) in the control zone (**I**) and the colony (**II-V**) of the great cormorants in Naudžiūnai, 2016–2019.

Species	**I**	**II-V**	**Total, n (%)**
S. araneus	0	2	2 (0.8%)
S. minutus	0	1	1 (0.4%)
M. glareolus	29	88	117 (44.7%)
A. agrarius	0	23	23 (8.8%)
A. flavicollis	39	80	119 (45.4%)
Total	**68**	**194**	**262**
Shannon's H	0.984	1.516	1.429
Simpson's c	0.511	0.39	0.414
RA±SE	8.50±1.36	22.75±4.35	15.63±2.58

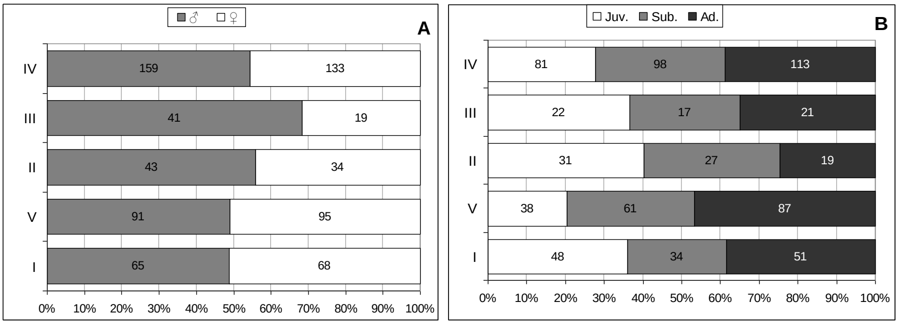

Fig. 4. Sex (A) and age (B) structure of *A. flavicollis* trapped in different zones of **JCC**. Zones: I – control, II – initial influence, III – long-term influence, IV – former active influence, V – ecotone.

Sex ratios of *M. glareolus* in **JCC** was significantly shifted towards males in zone III (76.5%) (more than in control zone, $\chi2=45.2$, $p<0.001$). As in the case described above only in zone III the difference from 1:1 sex ratio was significant ($\chi2=28.1$, $p<0.001$). In the zones V and IV sex ratios of *M. glareolus* were near 1:1. In the control zone females prevailed (56.8%), however, not significantly (Fig. 5A). The greatest proportion of juveniles (64.7%) and the smallest proportion of adults (23.5%) was found in zone III ($\chi2=23.8$, $p<0.001$; Fig 5B). In immature (juvenile and subadult) *M. glareolus* females prevailed (males 60.7%, females 39.3%). In the zones II, IV and V sex ratios were near 1:1. In the zone III the proportion of males was significantly higher 84.6% (compared to control, $\chi2=86.1$, $p<0.001$).

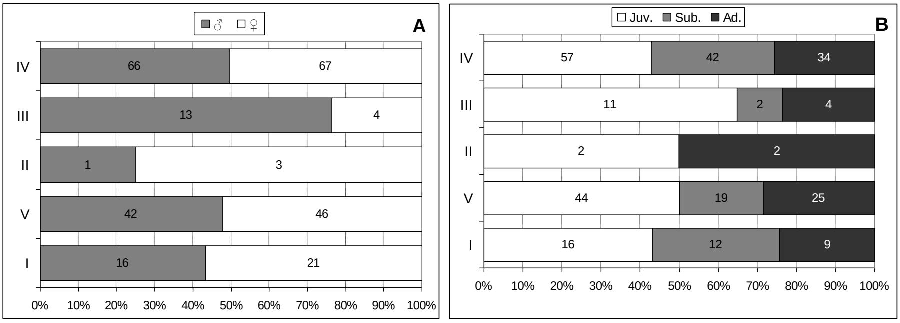

Fig. 5. Sex (A) and age (B) structure of *M. glareolus* trapped in different zones of **JCC**. Zones: I – control, II – initial influence, III – long-term influence, IV – former active influence, V – ecotone.

In **LCC** sex ratio of *A. flavicollis* was 1:1 both in the control (χ2=0.41, p=0.52) and the colony (χ2=0.16, p=0.69) (Fig. 6A). Colony was characterized by greater proportion of adults (52.0%) than control zone (42.6%) (χ2=10.1, p<0.01; Fig. 6B). The percentage of *M. glareolus* males in **LCC** was different among the colony (41.1%) and control (52.4%) zones (χ2=5.2, p<0.05; Fig. 6C). The shares of adult *M. glareolus* males in control and colony were similar (respectively 41.1% and 40.7%). The percentage of immature (juvenile and subadult) males of in the control differed from that in the colony (41.1% and 55.9%, respectively; χ2=9.0, p<0.01). Difference in age structure was not significant (χ2=1.6, p=0.46) (Fig. 6D).

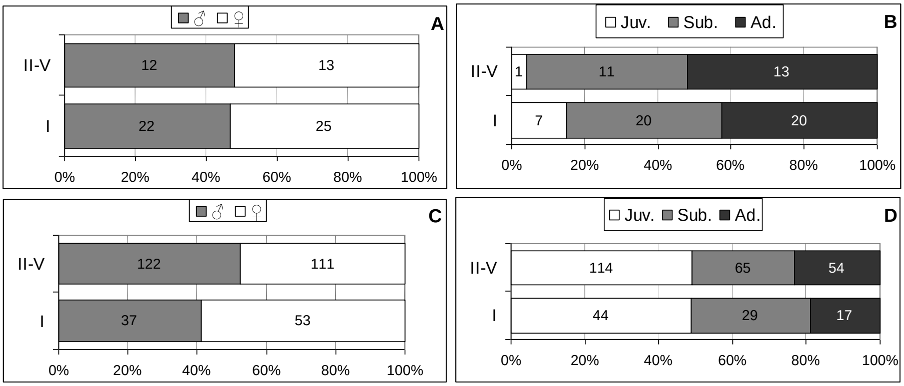

Fig. 6. Sex (A) and age (B) structure of *A. flavicollis* and sex (C) and age (D) structure of *M. glareolus* trapped in **LCC**: I – control, II-V – colony.

In **NCC** percentage of males of *A. flavicollis* was greater in control (61.5%) than in the colony (51.3%) (χ2=4.4, p<0.05; Fig. 7A). Proportion of adults (36.3%) in the colony was greater than in control (23.1%) (χ2=12.4, p<0.01; Fig. 7B).

In *M. glareolus* from **NCC** percentage of males significantly differed among the control zone (65.5%) and colony (42.5%) (χ2=23.4, p<0.001; Fig. 7C). In control difference from 1:1 sex ratio was significant (χ2=9.6, p<0.05). Most of the individuals caught in both the control zone (75.9%) and the colony (71.3%) were juveniles. However, proportion of adults in colony (14.9%) was significantly higher, than in control zone (6.9%) (χ2=10.2, p<0.01) (Fig. 7D).

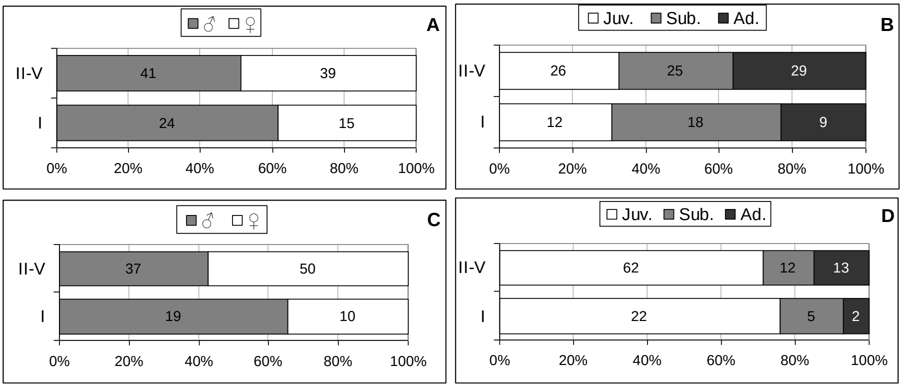

Fig. 7. Sex (A) and age (B) structure of *A. flavicollis* and sex (C) and age (D) structure of *M. glareolus* trapped in **NCC**: I – control, II-V – colony.

In **ECC** sex ratios of *M. glareolus* did not differ statistically from 1:1 in both control and colony (χ2=1.7, p=0.19). The proportion of adults in colony was higher (33.3%) than in control zone (14.3%) (χ2=25.8, p<0.001).

Paper II represents an initial investigation into sex and age structure of small mammal populations change in **JCC**.

Body condition index of small mammals is a proxy of the quality of environmental conditions. Worst average body condition of *A. flavicollis* in **JCC** was found in the active part of the colony (zone III, bc=3.35±0.07 (±SE); Table 6). It was reliably less than in zones I (bc=3.58±0.05; t=2.89, p<0.01) and IV (bc=3.51±0.03; t=2.16, p<0.05). Body condition difference between zones I and V (bc=3.46±0.03) was also significant (t=2.20, p<0.05).

In the zone of initial exposure, body condition of *A. flavicollis* males and females was affected differently (Fig. 8A). Females had a strong decrease of body conditions index in zone II (bc=3.34±0.09), whereas males have an increase (bc=3.65±0.11), difference significant (t=2.22, $p<0.05$). In other zones, there were no significant differences of body condition index between males and females. Body condition index in adult *A. flavicollis* showed no significant differences between the zones. Body condition index of juveniles and subadults in zone III (bc=3.32±0.10) was significantly lower than in zone IV (bc=3.53±0.05; t=1.99, $p<0.05$).

Table 6. Body condition indexes, average±SE, of *A. flavicollis* and *M. glareolus* in the colonies of great cormorants. Sample size is given in the brackets. Zones: I – control, II – initial influence, III – long-term influence, IV – former active influence, V – ecotone.

Colony	**Species**	**Zones**				
		I	**V**	**II**	**III**	**IV**
JCC	*A. fla*	3.58 ±0.05 (99)	3.46 ±0.03 (173)	3.52 ±0.08 (74)	3.35 ±0.07 (56)	3.51 ±0.03 (213)
	M. gla	3.09 ±0.09 (27)	3.28 ±0.05 (75)	2.94 ±0.06 (3)	2.85 ±0.09 (13)	3.43 ±0.06 (94)
LCC	*A. fla*	3.30 ±0.07 (47)	3.30±0.11 (25)			
	M. gla	3.03 ±0.05 (74)	3.14±0.04 (207)			
NCC	*A. fla*	3.40 ±0.10 (31)	3.64±0.08 (67)			
	M. gla	3.65 ±0.19 (14)	3.45±0.06 (73)			
ECC	*M. gla*	3.04 ±0.08 (21)	3.18±0.08 (24)			

The worst body condition of *M. glareolus* in **JCC** was found in zone II (bc=2.94±0.06) and zone III (bc=2.85±0.09). Body condition index in zone III was significant lower than in zone IV (bc=3.43±0.06; t=3.25, p<0.01) and V (bc=3.28±0.05; t=3.36, p<0.01). There were no gender differences in the body condition index (Fig. 8B). This index in adult *M. glareolus* showed no differences between the zones, though in juveniles and subadults from the zone III (bc=2.81±0.09) index was lower than in zone IV (bc=3.32±0.07; t=2.67, p<0.01) and zone V (bc=3.29±0.05; t=3.91, p<0.001).

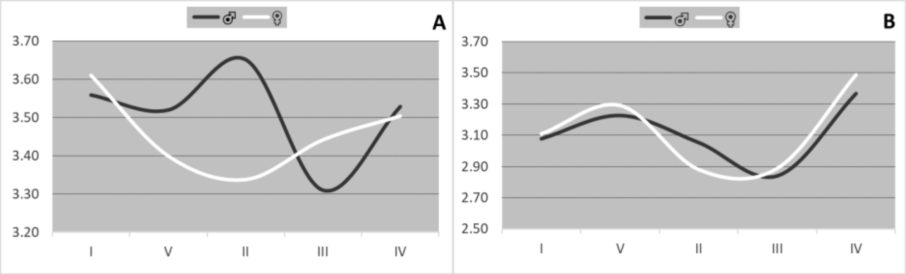

Fig. 8. The influence of the zone on body condition index of *A. flavicollis* (A) and *M. glareolus* (B) trapped in **JCC**, 2011–2019. Zones: I – control, II – initial influence, III – long-term influence, IV – former active influence, V – ecotone.

Body condition index of *A. flavicollis* in the **NCC** colony (bc=3.64±0.08) was insignificantly higher than in control (bc=3.40±0.10) (t=1.90, p=0.06). In **LCC** body condition index in *A. flavicollis* in colony and control was identical (Table 6) (t=0.05, p=0.95).

Body condition index in *M. glareolus* from **LCC, NCC** and **ECC** showed no statistically significant difference between the control and the colony (t=1.74, p=0.08; t=1.18, p=0.24; t=1.33, p=0.19, respectively).

Paper II presents results showing the influence of great cormorant colony into small mammal body condition in JCC.

The average ***litter size*** of *A. flavicollis* in **JCC** was 5.2±0.19 (±SE) (range 1–13), with an average of 4.7 embryos in the zone I to 6.0 in zone III (t=1.76, p=0.09). With the increasing influence of cormorants, the size of A. *flavicollis* litter increased (Table 7), but the differences were not statistically significant. The average litter size of *M. glareolus* in **JCC** was 4.2±0.27 (range 2–8), and ranged from an average of 3.7 embryos in zone V to 5.8 in zone I. In the control zone (I), litter size was of *M. glareolus* reliably greater than in zone V (t=2.40, p<0.05) and IV (2.41, p<0.05), thus, cormorant influence was negative. Data from zone II and III are characterized with insufficient sample size.

The average litter size of *A. flavicollis* in **LCC** was 5.0±0.47 (3–7) juveniles. In the colony litter size was higher (5.4±0.68) than in control (4.7±0.67), but difference was not significant (t=0.77, p=0.46). The same tendency was found in litter size of *M. glareolus* in **LCC**: in the colony (5.1±0.22) it was higher than in control (4.7±0.56), though the difference was not significant (t=0.73, p=0.47). In **NCC** and **ECC** colonies sample size of adult *A. flavicollis* and *M. glareolus* females was not sufficient (Table 7).

Table 7. Litter size, average±SE, of *A. flavicollis* and *M. glareolus* in the colonies of great cormorants. Sample size given in the brackets. Zones: I – control, II – initial influence, III – long-term influence, IV – former active influence, V – ecotone.

Colony	**Species**	**Zones**				
		I	**V**	**II**	**III**	**IV**
JCC	*A. flavicollis*	4.7±0.33 (21)	5.4±0.41 (32)	5.7±1.45 (3)	6.0±0.90 (7)	5.0±0.28 (43)
	M. glareolus	5.8±0.63 (4)	3.7±0.45 (11)	4.5±0.50 (2)	6.0±2.00 (2)	3.8±0.36 (17)
LCC	*A. flavicollis*	4.7±0.67 (6)	5.4±0.68 (5)			
	M. glareolus	4.7±0.56 (10)	5.1±0.22 (31)			
NCC	*A. flavicollis*	5.0±0.58 (3)	5.2±0.44 (11)			
	M. glareolus	(0)	4.6±0.84 (8)			
ECC	*M. glareolus*	3 (1)	3.5±1.5 (2)			

A. flavicollis and *M. glareolus* are dominant small mammal species in the forests of Lithuania (Balčiauskienė et al., 2009). All the studied cormorant colonies were dominated by these species (Tables 3–5). The average relative abundance of small mammals in the North Lithuania forests reached up to 25 ind./100 trap days (Alejūnas and Stirkė, 2010; Balčiauskas and Alejūnas, 2011) and fluctuated from 16 ind./100 trap days in forest stand to 36 ind./100 trap days in forest plantation (Jasiulionis et al., 2011). In this study, we found similar abundance in **JCC** zone V and IV, though in the active part of the cormorant colony (zones II, III), the abundance of these species was much lower (Table 3). Shannon's diversity index in the forests usually is not very high: H=1.06–1.90 in eastern

Lithuania (Mažeikytė, 2002); H=1.51 in Viešvilė Nature Reserve (Juškaitis and Uselis, 2005); H=1.14–2.09 in Pakruojis district (Jasiulionis et al., 2011); H=2.14 in the forests of northern part of Lithuania (Balčiauskas and Alejūnas, 2011). However, our study found much lower index (H=0.37) in the areas most affected by cormorants (**JCC** zone II). An earlier investigation indicated that forests in the Curonian Spit were extremely poor in species composition and abundance (Juškaitis and Ulevičius, 2002).

The numbers of species in the communities of small mammals are changing in habitats under succession (Jasiulionis et al., 2011). During meadow-forest succession processes, in most cases, the number of species decreased and dominance indexes increased (Čepukienė and Jasiulionis, 2012). In **JCC** we found similar tendency: with increasing exposure of the habitat to cormorants, dominance of *A. flavicollis* increased and the number of species decreased (Table 3). The abundance, species composition, and diversity of small mammals depend on vegetation composition, litter, sediments, tree canopy cover (Carey and Harrington, 2001), and all these environmental parameters are changing due to activity of cormorants (Klimaszyk and Rzymski, 2016). The impact of cormorant colonies on the forest can be compared to the changes caused by forest fire or clear-cut. In North America, the diversity of small mammals during succession after deforestation and after fire was similar: the abundance of small mammals increased with tree age and peaked in mature forests (Fisher and Wilkinson, 2005).

Biased sex ratio shows poor and disturbed habitat, or variation of the habitat quality over time (Julliard, 2000). Small mammal sex ratios potentially could be influenced by abundance, density, sex- dependent asynchronous mortality, exposure to extreme factors (Olenev and Grigorkina, 2011), and diet (Rosenfeld et al., 2003). An increased proportion of females was reported in the increase or peak phases of abundance (Myllymaki, 1977). Males were prevalent in both mice and voles as an outcome of heavy grazing (Bush et al., 2012). In disturbed habitats litters are male-biased (Ryan et al., 2012). Higher habitat quality is indicated with the higher proportion of adults (Millus and Stapp, 2008). In small sized colonies (**LCC**, **NCC**) we found lower proportion of adult *A. flavicollis* and *M. glareolus* in control than in colonies. In the biggest colony (**JCC**) the results were opposite: a smallest proportion of adult of both species was found in the active part of the colony, being higher in the control zone and in an abandoned part of the colony. In **NCC** higher proportion of males were found in the control zone than in colony for both dominant species (Fig. 7).

Body condition may depend on many factors including habitat quality and pollution (Alcantara and Diaz, 1996; Tête et al., 2013; Velickovic, 2007). Body condition has been found to correlate with fitness parameters, reproduction and survival. Lower body conditions of small mammals from polluted sites are interrelated by food availability and quality (Tête et al., 2013). Heavier animals have better competitive opportunities and are able to take habitats of higher quality. Moreover, individuals occupying top habitats become larger due to better nutrition and may resist to lighter immigrants from poorer habitats (Alcantara and Diaz, 1996). Body condition indexes of *A. flavicollis* and *M. glareolus* in **LCC**, **NCC** and **ECC** showed no significant differences between the control and the colony. However, in **JCC** highest body condition index of *M. glareolus* was found in areas with limited exposure of cormorants (zones V and IV), while it was lower in the active part of the colony (zones II and III) (Table 6). Similarly, worst body condition of *A. flavicollis* in **JCC** was found in the zone of long-term influence of the colony (III); body condition index was significantly lower than in control zone (I) or the zone of former active influence (IV).

Litter size of *A. flavicollis* we found in the cormorant colonies is similar to that identified across Europe: it was 5.7 in Spain (Gosalbez and Castian, 1995), 5.5 in Germany (Niethammer and Krap, 1978), 5.9–6.3 in Poland (Bobek, 1969). Litter size of *M. glareolus* is referenced as 4.2–6.0 (Bobek, 1969). In Lithuania, average litter size of *A. flavicollis* was referenced as 6.4, that of *M. glareolus* as 5.6 young (Prūsaitė et al., 1988). It is known that litter size is limited by food availability (Koskela et al., 1998) and stress (Wiebold et al., 1986). We found the only significant difference of litter size of *M. glareolus* in **JCC**, where it was larger in the control than in zones affected by cormorants.

Hence we may conclude that cormorant colonies with a small number of breeding birds had a positive effect on small mammals: number of species, relative abundance, proportion of adults and litter size increased (although the latter was not statistically significant). However, after reaching a high number of breeding birds, influence turned to strongly negative: species diversity, number of species, relative abundance, proportion of adults and body condition decreased, while dominance and proportion of males increased. Moreover, in a biggest colony impact on mammals was positive in the edge of the colony (ecotone) or in the abandoned part of the colony, where the number of nests was limited. Species diversity, number of species, relative abundance, proportion of adults and body condition in these zones were restored and even exceeded the respective values in the control zone.

High loads of the nutrients in the most heavily influenced zones of the big colony may affect small mammals in various ways: via altered plant composition (Veum et al., 2019), lack of shelter, disturbance, extremely high concentrations of nitrogen and phosphorus. Great cormorants can lead to enormous ecosystem transformation (Klimaszyk and Rzymski, 2016). Negative impacts of the colonies are not uncommon in plants (Matulevičiūtė et al., 2018), lichens (Zolkos et al., 2013), myxomycetes (Adamonytė et al., 2012). In the abandoned part of the big colony plants, shelter and food sources are restored. In the abandoned part of JCC diversity of myxomycetes had been partially restored (Adamonytė et al., 2013), and both nitrophilous lichens and those characteristic to mixed forests were recorded again (Motiejūnaitė et al., 2014).

As shown in other small mammals species (Velickovic, 2007; Tête et al., 2013), influence of the colony may be comparable to that of pollution. However, as soon as the disturbance factor is removed, small mammals are able to rapidly recover due to short generation time, intensive breeding and migration (Bush et al., 2012). So why influence of the small colonies are positive? In particular, extremely high levels of phosphorus and nitrogen do not accumulate in small colonies. Small amounts of cormorant faeces do not kill plants, they only fertilize the soil and change composition of the vegetation, allowing nitrophilic plants to grow. Grass cover and shrubs are usually more abundant in small cormorant colonies than in surrounding areas. They become excellent hiding places and a food source for small mammals. In addition, cormorants lose some of the fish brought to their young, thus replenishing the food resources of the mammals living there. Positive impacts of cormorant colonies were recorded for some species of insect, spider, lizard (Polis and Hurd, 1996) and herpetofauna (Kohno and Ota, 1991).

Long term data on the impact of the colonies of great cormorants on mammals enabled us suppose, that influence of cormorants on mammals depends on colony size. Topic was discussed with scientific community (Conference list, position 10). Unfortunately, these data we obtained are difficult to compare with other studies: other researchers typically select the largest bird colonies with extremely high environmental impacts. Further investigations of the small mammals in the colonies of great cormorants with the number of breeding pairs in the range of 300–3000 could show, what is the threshold in the number of birds for their influence to became negative.

4.2. Skull morphometry parameters change in cormorants colony

In **Paper III**, the skull morphometry in the two small mammal species (*A. flavicollis* and *M. glareolus)* trapped in different zones of the **JCC** was analysed. We found that sizes of *A. flavicollis* skull characters were significantly influenced by zone (Wilks λ=0.58, F=1.33, p<0.05). Differences of adult *A. flavicollis* in skull size between zones of the cormorants colony were significant for X3** (see **Paper III**, Material and methods) (ANOVA: *–p<0.05, **–p<0.01), X4*, X17* and X21* (**Paper III**, Fig. 1). In subadult *A. flavicollis* significant differences were found for the skull characters X2*, X3*, X5*, X13**, X15*, X16*, X19* and X21** (**Paper III**, Fig. 2). In juvenile *A. flavicollis*, there were no significant differences in skull measurements between zones. The size of the skull characters of *M. glareolus* did not differ significantly across the zones of the colony (Wilks λ=0.07, F=3.32, p=0.37). Differences in the skull size of adult *M. glareolus* between zones, however, were significant for some characters: X3*, X4*, X6*, X10* and X20** (**Paper III**, Fig. 4). No significant differences in skull measurements for subadult *M. glareolus* between zones were found. Contrary to the findings for *A. flavicollis*, the influence of the zone on the skull size of juvenile *M. glareolus* was present for many characters. Significant differences were found for X6*, X14*, X18*, X21* and X23*.

In general, most of the skull differences of both species were related to character length. Skulls tended to become longer in most active part of colony. The largest skull characters were recorded mostly in zone III (**Paper III**, Figs. 1–4). Mammals skull size differences may be driven by the gradient of pollution (Nunes et al., 2001; Fritsch et al., 2010; Tête et al., 2013) and also reflect the disturbance of the habitat or the influence of the stress level (Oleksyk et al., 2004; Velickovic, 2007; Hopton et al., 2009). By their influence on the environment, colonies of great cormorants may be considered as heavily polluted (Klimaszyk and Joniak, 2011; Klimaszyk et al., 2015). Moreover, in cormorant colonies small mammals are influenced by other stressors: the reduced amount of shelter due to damages of forest and grass cover, reduced food choices and the presence of predators visiting the colony for other items of food (**Paper VIII**).

Concluding, colony of cormorants had an influence on the skull morphometrics of *A. flavicollis* and *M. glareolus.* We presumed these differences were based on complex of factors in colony: bioaccumulation, reduced amount of shelters, reduced food choices and increased risk of predation.

4.3. Impact of cormorants on isotopic niche of small mammals

In **Paper IV** we show, that the highest δ^{15}N values in *M. glareolus* were observed in the largest colony of cormorants in Juodkrantė (17.86±2.76‰) exceeding those in the Lukštas (10.46±3.14‰) (Tukey HSD, $p<0.001$), Elektrėnai (12.62±2.07‰) colonies ($p<0.01$) and Lukštas (5.31±1.00‰), Elektrėnai (8.86±2.91‰), Zarasai (4.74±1.03‰) and Rusnė (6.38±0.95‰) control territories (all with $p<0.001$) (**Paper IV,** Fig. 3; **Paper VII,** Fig. 3). The average δ^{15}N values in the hair of *M. glareolus* from the Lukštas colony exceeded that in the Lukštas control territory (Tukey HSD, $p=0.0002$). δ^{15}N values in *M. glareolus* from the Zarasai and Rusnė control territories were significantly lower than from any other investigated colony (Tukey HSD, $p<0.05$–0.001) (**Paper IV,** Table 2; **Paper VII**). In Juodkrantė the lowest δ^{15}N values were registered in the hair of individuals trapped in the control zone (14.30‰), then higher in the ecotone (17.41±1.59‰) and highest in zone IV (18.22±0.92‰) (**Paper IV**).

The highest δ^{15}N values in *A. flavicollis* were observed in Juodkrantė colony (16.31±3.01‰). Average of δ^{15}N values in Juodkrantė colony were exceeding those in the Juodkrantė control territory (12.26±2.32‰) (Tukey HSD, $p<0.01$), Lukštas colony (5.46±0.37‰) ($p<0.001$) and Lukštas (4.06±0.71‰), Zarasai (5.04±0.95‰) control territories (both with $p<0.001$) (**Paper IV,** Fig. 2). In the control zones of the Juodkrantė δ^{15}N values in *A. flavicollis* were lower than in the zones influenced by cormorants: zone II (17.58±0.93‰) (Tukey HSD, $p<0.01$), zone III (17.05±0.73‰) ($p<0.001$), zone IV (16.14±1.37‰) ($p<0.001$) and zone V (15.89±0.49‰) ($p<0.01$) (**Paper IV,** Fig. 4).

The distribution of δ^{13}C values in *A. flavicollis* showed no significant differences between Juodkrantė colony (−24.19±0.48‰) and control zone (−24.20±0.17‰) as well as between Lukštas colony (−25.64±0.27‰) and control zone (−24.89±1.25‰). Average δ^{13}C value in *A. flavicollis* from the Lukštas colony (−25.64±0.27‰) was significantly lower than in the Juodkrantė colony (Tukey HSD, $p<0.01$) and Juodkrantė control territory ($p<0.05$). The highest δ^{13}C values were registered in the hair of the *M. glareolus* trapped in the cormorant colony in Juodkrantė (−24.88±0.97‰) and Juodkrantė control territory (−25.82‰), the former significantly higher than from all other sites (Tukey HSD, difference from the Elektrėnai colony (−26.08±0.67‰) ($p<0.05$), Elektrėnai (−26.02±0.79‰) ($p<0.01$) and Zarasai control territories (−26.74±0.63‰) ($p<0.001$) (**Paper IV,** Table 2).

The influence of the colony on isotopic niche of small mammals was recorded as early as in the first year after birds appear in the territory. An increase in the number of breeding pairs led to increased δ^{15}N values in *A. flavicollis*: 0.70‰ in expansion zone ($p<0.05$), 1.19‰ in ecotone ($p<0.05$) and 0.15‰ in active part of colony ($p>0.05$) (**Paper V**). Biogens transferred by great cormorants to the terrestrial ecosystem affected the potential foods of the small mammals and led to highly elevated and variable δ^{15}N values (**Paper V**).

Results of the **Paper IV** proved that the values of δ^{15}N in small mammals trapped in the territory of cormorant colonies were extremely high. These values were significantly higher than those in the individuals of the same species trapped in control areas. Moreover, the δ^{15}N values in *A. flavicollis* were dependent on the intensity and time of existence of the colony (**Paper IV, Fig. 4**). There is a slight possibility that the observed rodent enrichment in δ^{15}N was a result of eating cormorant tissues. Dead chicks, broken eggs and eggshells are constantly present on the ground underneath the nests in the breeding season, and so could serve as food source. It is known that in degraded forest ecosystems small mammals occupy higher trophic levels – disturbance leads to enrichment in of δ^{15}N in their tissues (Nakagawa et al., 2007). The high nitrogen stable isotope ratios observed in small mammals in the cormorant colonies could be explained by the “fertilization effect” on the environment.

Paper V concluded that possible food objects (plants and invertebrates) also were characterized by increased δ^{15}N values. We support the opinion of Millus and Stapp (2008) that changes on isotope niche of the small mammals in colonies were indirect, through influence on rodent food. High nitrogen stable isotopic ratios in cormorant colonies have been observed in other studies. For example, Kameda et al. (2006) reported unusually high nitrogen stable isotopic ratios in the forest floor and plant leaves in the abandoned colony. High nitrogen stable isotope ratios in seabird colonies have been explained by trophic enrichment and nitrogen decomposition processes (Lindeboom, 1984). Cormorants are the top predators in the aquatic trophic web (Bostrom et al., 2012). Nitrogen decomposition processes such as mineralization and nitrification also increase the nitrogen isotopic ratio in the soil (Nadelhoffer and Fry, 1988). The small range of nitrogen isotope ratios of *A. flavicollis* in the Lukštas colony and control territory and the Zarasai control territory suggested smaller fertilization effects on the feeding sources of *A. flavicollis*, at least in Zarasai forest. The small colony size in Lukštas resulted in limited biogen pollution, hence the low values of the stable nitrogen isotope.

4.4. Impact of cormorants on accumulation of chemical elements in small mammals

Paper VI represents the investigation into the accumulation of chemical elements in *A. flavicollis* trapped in different zones of great cormorants colony with different levels of impact. Zone was main factor determining the concentrations of chemical elements in *A. flavicollis* (MANOVA Wilks $\lambda=0.04$, $F_{3,53}=2.90$, $p<0.001$). Concentrations of K, Mn, Cu, Rb and Pb differed significantly between zones (**Paper VI,** Fig. 2). In the zones with higher levels of cormorant impact the concentrations of K and Cu increased, while Rb and Pb decreased. The overall impact of the influence of cormorants was positive: increases in the essential K, Cu and decrease in the harmful heavy metal Pb. Decrease in the essential microelement Rb was negative. Because Rb and K can replace each other, these chemical elements usually correlate negatively (Nyholm and Tyler, 2000).

Accumulation of five out of 20 investigated elements in the bodies of *A. flavicollis* inhabiting the territory of the great cormorants colony depended on the intensity of bird influence. However, as shown in **Paper VI**, this is hardly likely to be the sole reason for significant changes in small mammals (**Papers I–III**). Many ecological factors are changed due to the biological pollution in the colony, including the food base for the small mammals, the composition of vegetation, the presence of refuges. Chemical changes in the colony resulting from the transfer of materials from the aquatic to terrestrial ecosystem work in complex with these other changes. In general, the concentrations of accumulated potential harmful elements (Ni, Cu, Zn, Pb) in *A. flavicollis* from the territory of the cormorants colony were lower than in rodents from industrially polluted sites (Andras et al., 2006; Martiniaková et al., 2010; Martiniaková et al., 2015) (**Paper VI**, Table S3).

4.5. Seasonal and daily activity patterns of mammals in the colony of cormorants

In **Paper VIII**, we presented results of the analysis of seasonal and daily activity patterns in mammals, registered by camera traps in **LCC** and **JCC**. In **LCC** seasonal activity of *Vulpes vulpes* (t=4.39, p<0.001) and *Nyctereutes procyonoides* (t=3.74, p<0.001) was related to cormorant breeding season. Average relative shooting frequency of these carnivores in the breeding season (BT) was a few times higher than in non-breeding time (NT). Cormorant breeding season in **LCC** had no significant effect on *Capreolus capreolus* (t=0.76, p=0.47) and *Sus scrofa* (t=1.40, p=0.19) (**Paper VIII**, Fig. 3A). In **JCC** average relative shooting frequency of *V. vulpes* in BT was 2 times higher than in NT (t=2.31, p<0.05). Cormorant breeding season in **JCC** had no significant effect on *C. capreolus* (t=0.87, p=0.41) and *S. scrofa* (t=0.94, p=0.37) (**Paper VIII**, Fig. 3B).

Daily activity patterns of *S. scrofa* (χ2=47.7, p<0.001 in **LCC** and χ2=42.1, p<0.001 in **JCC**), *N. procyonoides* (χ2=45.2, p<0.001 in **LCC**) and *V. vulpes* (χ2=6.1, p<0.05 in **LCC** and χ2=20.0, p<0.001 in **JCC**) depended on cormorant activity (**Paper VIII**, Table 3). Cormorants feed the chicks during the daylight, and then they lose some of the prey. Consequently, more chicks accidentally fall out of the nests in the daytime. Daily activity patterns in mammals are internally regulated by external factors such as food accessibility (Masi et al., 2009; Diaz-Ruize et al., 2015). Predators like *V. vulpes* and *N. procyonoides* have to adapt to cormorant activity during the day.

N. procyonoides exhibits nocturnal activity (Akbaba and Ayas, 2012; Zoller and Drygala, 2013; Ikeda et al., 2016). In BT *N. procyonoides* was active in daytime (58.1% of all TE) and this was significantly differing from expected activity patterns, calculated by the time periods (χ2=8.14, df=2, p<0.05). In NT *N. procyonoides* activity peaks were registered at nighttime (70.0% of all TE; χ2=2.35, df=2, p=0.31) (**Paper VIII**, Table 3).

CONCLUSIONS

1. Small colonies of the great cormorants (80–130 breeding pairs) had a positive effect on ecological and biological parameters of small mammals: abundance, species richness, diversity and the proportion of adults increased.
2. In the biggest colony of great cormorants in Juodkrantė (1500–3800 breeding pairs) negative effects were most expressed in the active part of colony: abundance, species diversity, body condition index and proportion of females decreased, skull morphometry of *Apodemus flavicollis* and *Myodes glareolus* was affected. However, in the abandoned part and in the ecotone of the colony impact on small mammal ecological and biological parameters become positive: abundance, diversity and body condition index increased.
3. Disruption of the ecosystem caused by great cormorants affected isotopic niche of small mammals: $\delta^{15}N$ values were higher in rodents inhabiting all cormorant colonies. In the expansion zone of Juodkrantė colony cormorant influence was visible after the first year of nest appearance.
4. In the biggest colony in Juodkrantė, concentrations of K, Cu in *A. flavicollis* enlarged in line with an increase in the influence of the cormorants, while the concentrations of Rb and Pb decreased.
5. Eleven mammal species, including three non native ones, were camera-registered in great cormorant colonies of Juodkrantė and Lukštas. In the colony, the seasonal activity of *Vulpes vulpes* and *Nyctereutes procyonoides* was several times higher during the cormorant breeding season than at other times. In the breeding period of cormorants the daily activity of *Nyctereutes procyonoides*, *Vulpes vulpes* and *Sus scrofa* was altered, but no effects were found in *Capreolus capreolus*.

SCIENTIFIC AND PRACTICAL SIGNIFICANCE

Absence of the studies about the impact of cormorant colonies on mammals indicates that role of cormorants in the ecosystems is not known in details. Thus, results of this study allow a better assessment of the complexity of the environmental impact of cormorants. For the first time we highlighted the effect of colony size, finding that with increase of the colony positive effects are overweighed by the negative ones. We also find the immediacy of the colony impact, manifesting from the first year of nest appearance.

Our finding of the immediacy of impact of the colony has practical significance, showing that scaring birds from occupied areas can have a negative consequences. Scared cormorants make nests in other areas. Negative impact of an emerging new colony becomes visible in small mammals from the first year. Furthermore, results of the study allow planning of the “optimum” sizes of breeding colonies, based on the impact of birds to mammals. In Lithuania, cormorant abundance regulation activities are carried out if there are more than 100 breeding pairs in the colony. The results of our research showed that negative impact on the environment is not characteristic to the cormorant colonies not exceeding 200 breeding pairs.

SANTRAUKA

ĮVADAS

Darbo aktualumas. Smulkieji žinduoliai yra ekosistemų stabilumo indikatoriai, atliekantys svarbų vaidmenį daugelyje ekosistemų (Carey ir Harrington, 2001; Pearce ir Venier, 2005; Bogdziewicz ir Zwolak, 2014). Jie yra daugumos plėšriųjų paukščių ir žinduolių mitybinės grandinės pagrindas, užtikrinantis ekosistemų funkcionavimą (Jedrzejewski ir Jedrzejewska, 1992; Malecha ir Antczak, 2013; Wilson ir kt., 2017; Grabham ir kt., 2019; Gryz ir Krauze-Gryz, 2019). Rūšinė smulkiųjų žinduolių sudėtis ir gausumas nėra atsitiktiniai dydžiai, jie priklauso nuo aplinkos poveikio (Carey ir Harrington, 2001; Kozakiewicz ir Kozakiewicz, 2008). Rūšinę įvairovę, gausumą, dominavimą, lyčių ir amžiaus struktūrą bei kitus smulkiųjų žinduolių bendrijos rodiklius įtakoja aplinkos sąlygos. Keičiantis augalijos struktūrai, pomiškio ir medžių lajų sudėčiai bei paklotės sandarai, keičiasi ir smulkiųjų žinduolių bendrijos (Fox, 1995; Bryja ir kt., 2002; Briani ir kt., 2004; Čepukienė ir Jasiulionis, 2012). Dėl savo įvairiapusių ekologinių funkcijų smulkiesiems žinduoliams ypač svarbios yra nuokritos (Carey ir Harrington, 2001).

Neskaitant antropogeninio poveikio, didžiųjų kormoranų (*Phalacrocorax carbo*) kolonijos mūsų klimatinėje zonoje veikiausiai yra vienas sparčiausiai ir labiausiai aplinką keičiančių faktorių (Kameda ir kt., 2006; Klimaszyk ir Rzymsky, 2016). Kormoranai yra svarbus energijos ir daugelio cheminių elementų pernešėjas iš vandens į sausumos ekosistemas (Ellis ir kt., 2006; Otero ir kt., 2015). Įvairiapusis kormoranų poveikis aplinkai lemia visos ekosistemos transformaciją (Klimaszyk ir Rzymski, 2016).

Kormoranų įtaka žuvų ištekliams bei poveikis aplinkai perėjimo kolonijose kelia daug diskusijų visuomenėje. Žiniasklaida šiems paukščiams skiria daug dėmesio. Kormoranai ir jų poveikis aplinkai yra gerai žinomi, tačiau tyrimo, kuriame būtų nagrinėjama šių paukščių įtaka kolonijose aptinkamiems žinduoliams, iki šiol nebuvo. Disertacijos rengimo metu atlikti tyrimai prisidės vertinant kompleksinį kormoranų poveikį aplinkai.

DARBO TIKSLAS IR UŽDAVINIAI

Darbo tikslas buvo ištirti didžiųjų kormoranų (*Phalacrocorax carbo*) kolonijų poveikį smulkiųjų žinduolių ekologiniams ir biologiniams rodikliams bei įvertinti kormoranų kolonijų įtaką plėšriesiems ir kanopiniams žinduoliams.

Tikslui pasiekti buvo iškelti šie uždaviniai:

1. Ištirti ir įvertinti didžiųjų kormoranų kolonijų poveikį smulkiųjų žinduolių bendrijų sudėčiai, rūšinei įvairovei, gausumui, lyčių ir amžiaus struktūros kaitai, įmitimui ir morfometriniams rodikliams bei nustatyti, kaip šie rodikliai keičiasi priklausomai nuo kolonijos dydžio.
2. Įvertinti kormoranų perneštų biogenų įtaką smulkiųjų žinduolių izotopinei nišai, naudojant stabiliųjų izotopų santykio analizę.
3. Išanalizuoti sunkiųjų metalų ir kitų cheminių medžiagų kaupimąsi kolonijose gyvenančių smulkiųjų žinduolių audiniuose.
4. Įvertinti kormoranų veiklos įtaką plėšriųjų bei kanopinių žinduolių sezoniniam ir paros aktyvumui.

GINAMIEJI TEIGINIAI

1. Dėl kormoranų poveikio keičiasi smulkiųjų žinduolių bendrijų rūšinė sudėtis, gausumas, amžiaus ir lyčių struktūra, įmitimas bei kaukolės morfometriniai parametrai.
2. Teigiamas nedidelių kolonijų poveikis smulkiųjų žinduolių ekologiniams ir biologiniams parametrams didelėse kolonijose tampa neigiamu.
3. Iš vandens ekosistemų kormoranų perneštos maistinės medžiagos paveikia sausumos ekosistemų mitybos grandines ir smulkiųjų žinduolių izotopinę nišą.
4. Kormoranų kolonijos plėtra nedelsiant padidina biogenų kiekį sausumos ekosistemoje. Šis poveikis padidina stabiliųjų azoto izotopų vertes smulkiųjų žinduolių plaukuose.
5. Kormoranų kolonijų poveikis nėra toks stiprus kaip antropogeninės taršos šaltinių, tačiau įtakoja K, Cu, Rb ir Pb koncentraciją smulkiųjų žinduolių audiniuose.
6. Kormoranų kolonijos yra svarbios buveinės kai kuriems kanopiniams bei plėšriesiems žinduoliams. Kolonijose plėšriųjų žinduolių sezoninis ir paros aktyvumas dėl kormoranų veiklos pasikeičia.

DARBO NAUJUMAS

Šiame darbe pirmą kartą pasaulyje buvo visapusiškai įvertintas didžiųjų kormoranų poveikis žinduoliams. Tyrimas atskleidė kormoranų kolonijų įtaką smulkiųjų žinduolių bendrijų sudėčiai ir gausumui, populiacijų lyčių ir amžiaus struktūrai bei individų įmitimui. Nustatyta, kad teigiamas nedidelių kormoranų kolonijų poveikis ekologiniams ir biologiniams smulkiųjų žinduolių parametrams didelėse kolonijose keičiasi į neigiamą. Pirmą kartą išaiškinta, kad pakito dviejų kolonijoje gyvenančių smulkiųjų žinduolių rūšių kaukolės morfometrija. Taip pat pirmą kartą įvertinta kormoranų veiklos įtaka sunkiųjų metalų ir kitų cheminių elementų kaupimuisi žinduolių audiniuose bei atlikta anglies ($^{13}C/^{12}C$) ir azoto ($^{15}N/^{14}N$) stabiliųjų izotopų santykio analizė. Fundamentinis šio tyrimo naujumas buvo įrodymas, kad didžiųjų kormoranų kolonijos poveikis smulkiesiems žinduoliams pasireiškia jau pirmaisiais kolonijos susidarymo metais. Tyrimo rezultatai pirmą kartą parodė, kaip greitai pernešama biologinė tarša ir kaip ji pakeičia smulkiųjų žinduolių ekologiją. Be to, buvo nustatyti kanopinių ir plėšriųjų žinduolių rūšių paros bei sezoninio aktyvumo pokyčiai, vykstantys kolonijose perėjimo sezono metu.

Šis tyrimas leidžia geriau suvokti ilgalaikį kormoranų kolonijų poveikį ekosistemoms. Darbo rezultatai svarbūs vertinant kormoranų poveikį žinduoliams ir jų populiacijų parametrų pokyčius labai greitai kintančioje aplinkoje. Mūsų išvados prisideda prie biologinės taršos ir trikdžių bei kompleksinių aplinkos pokyčių kormoranų kolonijose vertinimo.

MEDŽIAGA IR METODIKA

Tyrimo vieta

Tyrimas buvo atliktas 4 Lietuvos didžiųjų kormoranų kolonijose: Juodkrantės, Lukšto, Naudžiūnų ir Elektrėnų (Table 1, Fig. 2). Juodkrantės kormoranų kolonijos teritorija pagal kormoranų daromo poveikio trukmę ir laipsnį buvo padalinta į penkias zonas (I straipsnis, Fig. 1; IV straipsnis, Fig. 1):

- ***Kontrolė*** (**I**) – zona kurioje nėra kormoranų poveikio;
- ***Pradinio kormoranų poveikio zona*** (**II**) – naujausia kormoranų kolonijos dalis, atsiradusi plečiantis kolonijai. Šioje zonoje medžiai vis dar gyvi, tačiau žolinė danga skurdesnė nei kontrolėje;
- ***Ilgalaikio kormoranų poveikio zona*** (**III**) – kormoranų kolonijos dalis, kurioje beveik visi medžiai nudžiūvę. Žolinė danga beveik išnykusi, užima iki 10% ploto. Šioje zonoje susitelkusi didžioji kormoranų kolonijos lizdų dalis;
- ***Ankstesnio kormoranų poveikio zona*** **(IV)** – teritorija, kurioje visi brandūs medžiai nudžiūvę, didžioji jų dalis nuvirtusi. Teritorija apaugusi jaunais medžiais, krūmais, žolinė danga vešli. Praeityje šioje zonoje kormoranų poveikis buvo intensyvus, tačiau, nuvirtus išdžiūvusiems medžiams, kormoranai išsikėlė;
- ***Ekotonas*** **(V)** – zona tarp kormoranų paveiktų ir nepaveiktų teritorijų (detaliau I straipsnyje).

Lukšto, Naudžiūnų ir Elektrėnų kolonijose buvo išskirtos kolonijos (**II-V**) ir kontrolės (**I**) zonos. Juodkrantės kormoranų kolonija perinčių paukščių skaičiumi yra didžiausia Lietuvoje ir viena didžiausių Europoje (mūsų tyrimo laikotarpiu čia perėjo nuo 1500 iki 3800 porų). Ją priskyrėme prie didelių kolonijų. Lukšto (iki 130 perinčių porų), Naudžiūnų (iki 80) ir Elektrėnų (iki 160) priskyrėme prie mažųjų kolonijų.

Smulkiųjų žinduolių bendrijų tyrimai

Smulkieji žinduoliai buvo gaudomi naudojant mušamųjų spąstų linijas, kurių kiekvienoje buvo 25 spąstai, išdėstyti 5 metrų atstumu vienas nuo kito. Masalui naudotas džiovintos tamsios duonos kubelis, suvilgytas nerafinuotame saulėgrąžų aliejuje. Spąstai laikyti nuo 1 iki 3 parų, tikrinami kiekvieną dieną (Balčiauskas, 2004). Tyrimo apimtis visose 4 kormoranų kolonijose – 17700 spąstų-parų (257 spąstų linijos). Tyrimas vykdytas 2011–2019 metais, rugsėjo–lapkričio mėnesiais. Juodkrantės kormoranų kolonijoje 2013 ir 2014 metais buvo papildomai gaudoma birželio mėnesį. Buvo apibūdinama žvėrelių rūšis, prieš skrodimą jie pasveriami, pamatuojami, skrodžiant nustatomas amžius ir lytis (II straipsnis). Santykinis smulkiųjų žinduolių gausumas apskaičiuotas pagal pagautų individų skaičių per pirmą parą su 100 spąstų (ind./100 sp. p.). Darbe naudojome Šenono (Shannon's) įvairovės bei Simpsono dominavimo indeksus. Smulkiųjų žinduolių įmitimo indeksas buvo paskaičiuotas pagal formulę $bc=(Q/L^3)\times10^5$, kur Q – kūno svoris (gramais), L – ilgis (milimetrais) (Moors, 1985).

Kaukolių morfometrija

Naudojant binokuliarinį mikroskopą su matavimo skale išmatuoti 468 geltonkaklės pelės (*Apodemus flavicollis)* ir 151 rudojo pelėno *(Myodes glareolus)* individų 23 kaukolės matmenys (III straipsnis).

Stabiliųjų izotopų analizė

Stabiliųjų izotopų analizei buvo pasirinktos dvi dažniausiai kolonijose pagautos smulkiųjų žinduolių rūšys: *A. flavicollis* (ištirti 129 individai) ir *M. glareolus* (120 individų). Analizei buvo naudojami žvėrelių plaukai. Nuo kiekvieno individo nugaros nukirptų plaukų kuokštelis buvo laikomas plastikiniame maišelyje. Prieš atliekant analizę plaukai buvo pasverti ir sudėti į alavo kapsules. Augalų, bestuburių ir nuokritų mėginiai 24–48 valandas džiovinami džiovinimo krosnyje 60 °C temperatūroje iki orasausės masės, po to homogenizuoti naudojant agato trintuvę ir maišytuvą Retsch MM 400. Matavimai atlikti naudojant elementinį analizatorių (Flash EA1112), sujungtą su izotopų santykio masių spektrometru (Thermo Delta V Advantage, Thermo Scientific, USA) (IV, V, VII straipsniai). Stabiliųjų izotopų duomenys pateikti kaip δ vertės apskaičiuotos pagal formulę:

$$\delta X=(R_{sample}/R_{standard}-1)*10^3,$$

kur $R_{sample}={}^{13}C/{}^{12}C$ arba ${}^{15}N/{}^{14}N$, $R_{standard}={}^{13}C/{}^{12}C$ arba ${}^{15}N/{}^{14}N$ (IV, V, VII straipsniai).

Cheminių elementų tyrimas

Cheminiai elementai išanalizuoti Juodkrantės kormoranų kolonijoje pagautų *A. flavicollis* (54 individai) audiniuose. Ištirta 20 cheminių elementų koncentracija: Na, Mg, Al, Si, P, S, Cl, K, Ca, V, Mn, Fe, Ni, Cu, Zn, Br, Rb, Sr, Mo ir Pb. Audiniai buvo džiovinami 100 °C, po to deginami 240 °C temperatūroje. Gauti pelenai susmulkinti maišytuve Retsch MM 400 ir sumaišyti su rišamąja medžiaga Licowax (Fluxana) santykiu 1,25 g pelenų ir 0,28 g rišamosios medžiagos. Po to kiekvienas pavyzdys buvo homogenizuojamas ir suspaudžiamas į 20 mm diametro tabletes naudojant 15 KN (presas PP25). Analizė atlikta SPECTRO XEPOS HE spektrometru (VI straipsnis).

Gyvūnų registravimas žvėrių stebėjimo kameromis

Žinduolių aktyvumas vertintas naudojant Ltl Acorn-5210A žvėrių stebėjimo kameras. Tyrimas vykdytas Juodkrantės (tyrimo apimtis 1370 parų) ir Lukšto (1317 parų) kormoranų kolonijose. Kameros buvo tvirtinamos prie medžių, 40–60 cm aukštyje. Šios kameros automatiškai registruoja laiką ir datą. Metai buvo padalinti į du periodus: kormoranų veisimosi laikotarpis (balandis–liepa) (BT) ir ne veisimosi laikotarpis (rugpjūtis–kovas) (NT). Para padalinta į 3 dalis: diena (D), naktis (N) ir prieblanda (T). Prieblanda laikomas laiko tarpas 60 minučių prieš saulėtekį ir 60 min. po saulėtekio, bei 60 min. prieš saulėlydį ir 60 min. po saulėlydžio. Diena – laikotarpis nuo 60 min. po saulėtekio iki 60 min. iki saulėlydžio. Naktis – laikotarpis nuo 60 min. po saulėlydžio iki 60 min. iki saulėtekio (VIII straipsnis).

Statistinė analizė

Statistinė analizė atlikta naudojant STATISTICA 6 programą. Duomenų analizėje naudotas kritinis patikimumo lygmuo $p \leq 0{,}05$. Vidurkiai pateikti nurodant standartinę paklaidą (±SE). Skirtumų analizei naudoti t testas, vienfaktorinė bei daugiafaktorinė ANOVA, neparametriniai $\chi 2$, Kruskal-Wallis testai. Duomenų atitikimas normaliajam skirstiniui vertintas Kolmogorovo-Smirnovo testu.

REZULTATAI IR APTARIMAS

Per 9 tyrimo metus keturiose kormoranų kolonijose pagauti 1967 smulkiųjų žinduolių individai, priklausantys 10 rūšių: paprastasis kirstukas (*Sorex araneus*), kirstukas nykštukas (*S. minutus*), vandeninis kirstukas (*Neomys fodiens*), *M. glareolus*, pievinis pelėnas (*Microtus agrestis*), pelkinis pelėnas (*M. oeconomus*), naminė pelė (*Mus musculus*), pelė mažylė (*Micromys minutus*), dirvinė pelė (*Apodemus agrarius*) ir *A. flavicollis*.

Visose Juodkrantės kormoranų kolonijos poveikio zonose dominuojanti smulkiųjų žinduolių rūšis buvo *A. flavicollis*, subdominuojanti – *M. glareolus*. Daugiausia rūšių pagauta ankstesnio poveikio zonoje (IV) (7 rūšys), kontrolėje (I) (6 rūšys) ir ekotone (V) (5 rūšys). Aktyvaus kormoranų poveikio zonose (II ir III) aptiktas mažesnis rūšių skaičius (atitinkamai 3 ir 4). Aktyvaus poveikio zonose nustatytas ir mažesnis smulkiųjų žinduolių gausumas (II – 4,65±1,08 ind./100 sp. p.; III – 4,76±1,41) nei kontrolėje (10,38±1,51), ekotone (20,96±2,82) ar ankstesnio poveikio zonoje (22,46±1,85). Lukšto kormoranų kolonijoje sugautų žvėrelių rūšių skaičius buvo didesnis nei kontrolėje (atitinkamai 9 ir 6 rūšys). Santykinis gausumas kolonijoje (29,17±2,92 ind./100 sp. p) daugiau nei 2 kartus viršijo gausumą kontrolinėje zonoje (13,50±2,14; $t=4,33$, $p<0,001$). Tokia pati tendencija nustatyta Naudžiūnų kormoranų kolonijoje, kur rūšių skaičius buvo mažesnis nei kontrolėje (atitinkamai 2 ir 5 rūšys). Skyrėsi ir santykinis gausumas, 8,50±1,36 ind./100 sp. p. kontrolėje ir 22,75±4,35 kolonijoje ($t=3,13$, $p<0,01$). Elektrėnų saloje esančioje kormoranų kolonijoje ir kontrolėje sugauta vienintelė smulkiųjų žinduolių rūšis – *M. glareolus.* Šioje teritorijoje žvėrelių gausumas kolonijoje (7,00±2,36 ind./100 sp. p.) ir kontrolėje (8,00±2,73) nesiskyrė ($t=0,28$, $p=0,79$).

Juodkrantės kormoranų kolonijoje sugautų *A. flavicollis* lyčių struktūra kontrolėje ir ekotone buvo identiška: abiejose zonose patinai sudarė 48,9%, patelės – 51,1%. Kitose zonose dominavo patinai, nors, lyginant su kontrole, skirtumas ne visais atvejais buvo patikimas: IV zonoje patinų buvo 54,5% ($\chi2=1,26$, $p=0,26$), II zonoje – 55,8% ($\chi2=1,91$, $p=0,17$), III zonoje – 68,3% ($\chi2=15,1$, $p<0,01$). Vieninteléje III zonoje lyčių struktūra patikimai skyrėsi nuo 1:1 ($\chi2=13,4$, $p<0,001$). *A. flavicollis* amžiaus struktūra kormoranų paveiktose Juodkrantės kolonijos vietose skyrėsi: II zonoje vyravo jaunikliai (40,3%) ir lytiškai nesubrendę individai (35,0%), V zonoje – suaugėliai (46,8%). *M. glareolus* lyčių struktūra Juodkrantės kolonijos ilgalaikio kormoranų poveikio zonoje (III) skyrėsi nuo kontrolės ($\chi2=45,2$, p<0,001) ir nuo santykio 1:1 (χ2=28,1, p<0,001). III zonoje patinų dalis populiacijoje buvo beveik 2 kartus didesnė, nei kontrolėje (atitinkamai 76,5% ir 43,2%).

Lukšto kolonijoje *A. flavicollis* lyčių struktūra kontrolėje ir kolonijoje buvo artima santykiui 1:1. Kolonijai buvo būdinga didesnė suaugėlių (52,0%) bei mažesnė jauniklių (4,0%) dalis nei kontrolėje (atitinkamai 42,6% ir 14,9%; χ2=10,1, p<0,01). Lytiškai nesubrendusių individų dalis kontrolėje (42,6%) ir kolonijoje (44,0%) buvo panaši.

Naudžiūnų kolonijoje *A. flavicollis* patinų dalis kontrolėje buvo didesnė nei kolonijoje (atitinkamai 61,5% ir 51,3%; χ2=4,4, p<0,05). Suaugusių *A. flavicollis* individų dalis kolonijoje buvo didesnė nei kontrolėje (36,3% ir 23,1%; χ2=12,4, p<0,01). Naudžiūnų kolonijoje tos pačios tendencijos nustatytos *M. glareolus*. Patinų dalis kolonijoje buvo didesnė nei kontrolėje (atitinkamai 65,5% ir 42,5%; χ2=23,4, p<0,001). Kolonijoje suaugusių individų buvo daugiau negu kontrolėje (14,9% ir 6,9%; χ2=10,2, p<0,01). *M. glareolus* lyčių struktūros skirtumų tarp kolonijos ir kontrolės Elektrėnų kolonijoje nebuvo. Suaugusių individų kolonijoje buvo daugiau nei kontrolėje (33,3% ir 14,3%; χ2=25,8, p<0,001).

Mažiausias *A. flavicollis* įmitimo indeksas Juodkrantės kormoranų kolonijos ilgalaikio poveikio zonoje (III) (bc=3,35±0,07) buvo patikimai mažesnis nei kontrolinėje zonoje (bc=3,58±0,05; t=2,89, p<0,01). Tačiau Naudžiūnų kormoranų kolonijoje *A. flavicollis* įmitimas buvo didesnis nei kontrolėje (atitinkamai bc=3,64±0,08 ir 3,40±0,10), bet skirtumas nepatikimas (t=1,90, p=0,06). Juodkrantės kolonijoje prasčiausias *M. glareolus* įmitimas nustatytas aktyvaus kormoranų poveikio zonose (II – bc=2,94±0,06; III – bc=2,85±0,09). Patikimi skirtumai rasti tarp III zonos ir IV (bc=3,43±0,06; t=3,25, p<0,01) bei V (bc=3,28±0,05; t=3,36, p<0,01) zonų. Lukšto, Naudžiūnų ir Elektrėnų kolonijose *M. glareolus* įmitimo indeksas kontrolėje ir kolonijoje nesiskyrė.

Juodkrantės kormoranų kolonijoje *M. glareolus* vidutinis vados dydis kontrolinėje zonoje buvo patikimai didesnis nei ekotone (V) (atitinkamai 5,8±0,63 ir 3,7±0,45; t=2,40, p<0,05) ir buvusio poveikio zonoje (IV) (3,8±0,36; t=2,41, p<0,05). Kitose kormoranų kolonijose patikimų skirtumų tarp kolonijos ir kontrolės nenustatyta.

Apibendrinant galime teigti, kad nedaug perinčių paukščių turinčių kormoranų kolonijų poveikis smulkiesiems žinduoliams buvo teigiamas: padidėjo rūšių skaičius, santykinis gausumas, suaugusiųjų individų dalis bendrijoje bei vados dydis (nors vados dydžio pasikeitimas nėra statistiškai reikšmingas). Tačiau kormoranų kolonijai pasiekus tam tikrą dydį poveikis tampa neigiamas: sumažėja smulkiųjų žinduolių rūšių skaičius, įvairovė, santykinis gausumas, suaugusių individų dalis ir įmitimas, padidėja vienos rūšies dominavimas bendrijoje bei patinų dalis. Tačiau netgi didelėse kolonijose kormoranų poveikis žinduoliams gali būti teigiamas kolonijos pakraštyje (ekotone) arba apleistoje kolonijos dalyje, kur lizdų skaičius ribotas. Šiose zonose rūšinė įvairovė, rūšių skaičius, santykinis gausumas, suaugusiųjų individų dalis ir įmitimo indeksas atsistato ir netgi padidėja, lyginant su kontroline zona.

Labiausiai paveiktose didelių kolonijų zonose įtaka smulkiesiems žinduoliams galima dėl pakitusios augalijos sudėties (Veum ir kt., 2019), slėptuvių stokos, trikdymo, bei neįprastai didelės azoto ir fosforo koncentracijos. Kormoranai gali stipriai pakeisti aplinką, kurioje gyvena (Klimaszyk ir Rzymski, 2016). Neigiamas kolonijų poveikis nustatytas augalams (Matulevičiūtė ir kt., 2018), kerpėms (Zolkos ir kt., 2013), miksomicetams (Adamonytė ir kt., 2012). Tačiau apleistoje Juodkrantės kolonijos dalyje miksomicetų bei kerpių įvairovė dalinai atsistatė (Adamonytė ir kt., 2013; Motiejūnaitė ir kt., 2014). Atsikuriant augalijai, apleistose kolonijų dalyse padaugėja slėptuvių bei maisto išteklių smulkiesiems žinduoliams. Kai tik pašalinamas trikdžių faktorius, jų bendrijos dėl didelio reprodukcijos greičio bei migracijos geba greitai atsistatyti (Bush ir kt., 2012).

Kodėl mažose kolonijose kormoranų poveikis smulkiesiems žinduoliams yra teigiamas? Pirmiausia, jose nesusikaupia ekstremaliai didelės azoto ir fosforo koncentracijos. Nedideli kormoranų išmatų kiekiai tik patręšia dirvą ir pakeičia augalijos sudėtį, bet jos nesunaikina. Mažose kolonijose žolinė danga ir krūmai būna vešlesni nei aplinkinėse, kormoranų nepaveiktose teritorijose. Suvešėję augalai tampa puikiomis slėptuvėmis ir maisto šaltiniu smulkiesiems žinduoliams. Be to, žinduolių mitybos racioną papildo kormoranų pamestos žuvys bei iš lizdų iškritę jaunikliai.

III straipsnyje analizuojami Juodkrantės kolonijoje sugautų *A. flavicollis* ir *M. glareolus* kraniometrinių rodiklių skirtumai. Nustatėme, kad skirtingo kormoranų poveikio intensyvumo zonose *A. flavicollis* kraniometriniai rodikliai skyrėsi patikimai (Wilks $\lambda=0,58$, $F=1,33$, $p<0,05$). Patikimai (ANOVA: *–$p<0,05$, **–$p<0,01$) skyrėsi šie suaugusių *A. flavicollis* kaukolių matmenys: X3** (žiūrėti III straipsnį, Material ir methods), X4*, X17* ir X21* (III straipsnis, Fig. 1). Taip pat patikimai skyrėsi ir lytiškai nesubrendusių *A. flavicollis* individų kaukolių X2*, X3*, X5*, X13**, X15*, X16*, X19*, X21** matmenų dydžiai (III straipsnis, Fig. 2). Jauniklių *A. flavicollis* kraniometriniai rodikliai tarp skirtingų poveikio zonų nesiskyrė. Kolonijos zonos įtaka antros pagal gausumą rūšies *M. glareolus* kaukolės matmenims nebuvo patikima (Wilks λ=0,07, F=3,32, p=0,37). Tačiau kai kurie suaugusių (X3*, X4*, X6*, X10*, X20**; III straipsnis, Fig. 4) ir jauniklių (X6*, X14*, X18*, X21*, X23*) kaukolių matmenys skyrėsi patikimai. Nustatyta, kad kormoranų poveikio zonose *A. flavicollis* ir *M. glareolus* kaukolės pailgėja. Labiausiai kraniometriniai rodikliai skyrėsi ilgalaikio kormoranų poveikio zonoje (III straipsnis, Figs. 1–4).

Žinduolių kraniometriniai rodikliai gali pakisti dėl taršos (Nunes ir kt., 2001; Fritsch ir kt., 2010; Tête ir kt., 2013), trikdymo ir streso (Oleksyk ir kt., 2004; Velickovic, 2007; Hopton ir kt., 2009). Didžiųjų kormoranų kolonijų teritorijos gali būti laikomos labai užterštomis (Klimaszyk ir Joniak, 2011; Klimaszyk ir kt., 2015). Be to, jose smulkiuosius žinduolius veikia kiti stresoriai: dėl sunykusios žolinės dangos sumažėjęs slėptuvių kiekis, mažesnis maisto pasirinkimas, padidėjęs plėšrūnų skaičius (VIII straipsnis). Taigi, *A. flavicollis* ir *M. glareolus* morfometrinių kaukolės rodiklių skirtumai atsiranda dėl kompleksinio kormoranų kolonijų poveikio (III straipsnis).

IV, V ir VII straipsniuose analizuojami *M. glareolus* ir *A. flavicollis* stabiliųjų izotopų (δ^{15}N ir δ^{13}C) santykio skirtumai Juodkrantės, Lukšto, Elektrėnų kormoranų kolonijose bei Lukšto, Elektrėnų, Zarasų ir Rusnės kontrolėje. Nustatėme, kad didžiausioje Juodkrantės kormoranų kolonijoje *M. glareolus* δ^{15}N vertės buvo patikimai didesnės, nei Lukšto kolonijoje (Tukey HSD, p<0,001), Elektrėnų kolonijoje (p<0,01) bei Lukšto, Elektrėnų, Zarasų, Rusnės kontrolinėse teritorijose (visų p<0,001; IV straipsnis, Fig. 3; VII straipsnis, Fig. 3). Lukšto kolonijoje sugautų *M. glareolus* plaukuose vidutinės stabiliųjų azoto izotopų (δ^{15}N) vertės buvo didesnės negu kontrolės zonos individų (Tukey HSD, p=0,0002). Aukščiausios *A. flavicollis* δ^{15}N vertės nustatytos Juodkrantės kolonijoje. Vidutinės δ^{15}N vertės Juodkrantės kolonijoje buvo patikimai didesnės, nei Juodkrantės kontrolinėje zonoje (Tukey HSD, p<0,01), Lukšto kolonijoje (p<0,001) bei Lukšto ir Zarasų kontrolėje (p<0,001) (IV straipsnis, Fig. 2). *A. flavicollis* δ^{15}N vertės Juodkrantės kontrolinėje zonoje buvo mažesnės nei kormoranų paveiktose zonose: II poveikio zonoje (Tukey HSD, p<0.01), III zonoje (p<0,001), IV zonoje (p<0,001) ir V zonoje (p<0,01) (IV straipsnis, Fig. 4). Nustatėme, jog kormoranų kolonijai išsiplėtus į naujas teritorijas jau pirmaisiais invazijos metais keičiasi stabiliųjų izotopų santykis smulkiųjų žinduolių plaukuose. Didėjant perinčių kormoranų skaičiui didėja δ^{15}N ir mažėja δ^{13}C vertės (V straipsnis). Millus ir Stapp (2008) teigia, kad smulkiųjų žinduolių izotopinės nišos pokyčiai paukščių kolonijose yra įtakojami ne tiesiogiai, bet per maistą. Kormoranų perneštos biogeninės medžiagos veikia potencialų smulkiųjų žinduolių maistą, dėl to padidėja $\delta^{15}N$ reikšmės. Aukštas azoto stabiliųjų izotopų santykis buvo nustatytas kormoranų kolonijų paklotėje bei augalų lapuose (Kameda ir kt., 2006). Vandens ekosistemose kormoranai yra mitybos grandinės viršuje (Bostrom ir kt., 2012). Azoto skilimo procesai, pvz., mineralizacija ir nitrifikacija, taip pat padidina azoto izotopų santykį dirvožemyje (Nadelhoffer ir Fry, 1988).

VI straipsnyje išanalizuotas cheminių elementų kaupimasis *A. flavicollis* audiniuose Juodkrantės kormoranų kolonijoje. Nustatėme, jog poveikio zona yra pagrindinis veiksnys, lemiantis cheminių elementų koncentraciją (MANOVA Wilks $\lambda=0{,}04$, $F_{3{,}53}=2{,}90$, $p<0{,}001$). Skirtingose zonose pagautuose individuose K, Mn, Cu, Rb ir Pb koncentracija skyrėsi patikimai (VI straipsnis, Fig. 2). Intensyvesnio poveikio zonose K ir Cu koncentracijos buvo didesnės, Rb ir Pb – mažesnės. Kormoranų įtaka buvo teigiama, nes padidėjo naudingų mikroelementų (K ir Cu) koncentracijos ir sumažėjo kenksmingo sunkiojo metalo Pb koncentracija. Sumažėjusi Rb koncentracija spėjamai yra susijusi su K koncentracijos padidėjimu, kadangi šie 2 mikroelementai vienas kitą pakeičia; todėl organizme jų koncentracijos dažnai koreliuoja neigiamai (Nyholm ir Tyler, 2000). Apibendrinant, penkių iš 20 ištirtų cheminių elementų koncentracijos *A. flavicollis* audiniuose priklausė nuo kormoranų poveikio intensyvumo. Tikėtina, kad aukščiau aprašytus smulkiųjų žinduolių bendrijų sudėties, rūšinės įvairovės, gausumo, lyčių ir amžiaus struktūros, įmitimo bei kraniometrinių rodiklių pokyčius nulėmė ne vien tik cheminių elementų koncentracijos audiniuose. Dėl taršos kormoranų kolonijose pasikeičia augalija, nuo kurios priklauso ir slėptuvių skaičius bei maisto ištekliai. Šie veiksniai kartu su pertekliniu kormoranų atneštų medžiagų kiekiu veikiausiai ir sąlygoja pokyčius smulkiųjų žinduolių bendrijoje.

VIII straipsnio rankraštyje analizuojami žinduolių sezoninio ir paros aktyvumo pokyčiai Lukšto ir Juodkrantės kormoranų kolonijose. Naudojant žvėrių stebėjimo kameras nustatyta, kad Lukšto kolonijoje lapių (*Vulpes vulpes)* ir mangutų (*Nyctereutes procyonoides)* sezoninis aktyvumas priklausė nuo kormoranų perėjimo sezono (atitinkamai t=4,39, p<0,001 ir t=3,74, p<0,001). Vidutinis šių žinduolių registravimo dažnumas kormoranų veisimosi laikotarpiu buvo kelis kartus didesnis. Lukšto kolonijoje kormoranų perėjimas stirnų (*Capreolus capreolus)* (t=0,76, p=0,47) ir šernų *(Sus scrofa)* (t=1,40, p=0,19) aktyvumui įtakos neturėjo (VIII straipsnis, Fig. 3A).

Juodkrantės kolonijoje *V. vulpes* aktyvumas buvo 2 kartus didesnis kormoranų perėjimo laikotarpiu (t=2,31, p<0,05). Tačiau, kaip ir Lukšto kolonijoje, *C. capreolus* (t=0,87, p=0,41) ir *S. scrofa* (t=0,94, p=0,37) sezoniniam aktyvumui perėjimo laikotarpis įtakos neturėjo (VIII straipsnis, Fig. 3B**)**. Lukšto kormoranų kolonijoje *S. scrofa*, *N. Procyonoides* ir *V. vulpes* paros aktyvumas priklausė nuo kormoranų aktyvumo (atitinkamai χ2=47,7 ir χ2=45,2, p<0,001 bei χ2=6,1, p<0,05). Juodkrantės kolonijoje nuo kormoranų aktyvumo priklausė *S. scrofa* ir *V. vulpes* paros aktyvumas (atitinkamai χ2=42,1 ir χ2=20,0, p<0,001; VIII straipsnis, Table 3).

Žinduolių paros ritmą keičia maisto prieinamumas (Masi ir kt., 2009; Diaz-Ruize ir kt., 2015). Kormoranai jauniklius maitina dienos metu ir pameta dalį atnešto maisto. Be to, kai kurie neskraidantys jaunikliai iškrenta iš lizdų. Pamestos žuvys bei iškritę jaunikliai tampa lengvu grobiu plėšriesiems žinduoliams. *N. procyonoides* yra naktiniai gyvūnai (Akbaba ir Ayas, 2012; Zoller ir Drygala, 2013; Ikeda ir kt., 2016). Komoranams neperint, Lukšto kolonijoje tik 20,0% atvejų *N. procyonoides* buvo registruoti dienos metu. Pradėjus perėti, net 58,1% atvejų šie gyvūnai buvo registruoti dieną (VIII straipsnis, Table 3).

IŠVADOS

1. Mažos kormoranų kolonijos (80–130 perinčių porų) darė teigiamą įtaką smulkiųjų žinduolių ekologiniams ir biologiniams parametrams: didėjo santykinis jų gausumas, rūšių skaičius bei suaugusių individų dalis bendrijoje.
2. Didžiausios Lietuvoje Juodkrantės kormoranų kolonijos (1500–3800 perinčių porų) aktyvioje dalyje neigiamas poveikis smulkiųjų žinduolių bendrijai buvo labiausiai išreikštas: sumažėjo gausumas, rūšinė įvairovė, įmitimo indeksas, patelių dalis bendrijoje, pasikeitė geltonkaklių pelių (*Apodemus flavicollis*) ir rudųjų pelėnų (*Myodes glareolus*) kaukolės morfometriniai rodikliai. Apleistoje kormoranų kolonijos dalyje ir ekotone nustatytas teigiamas poveikis smulkiesiems žinduoliams: jų gausumas, įvairovė ir įmitimo indeksas padidėjo.
3. Didžiųjų kormoranų kolonijų sąlygota ekosistemos degradacija pakeitė smulkiųjų žinduolių izotopinę nišą – $\delta^{15}N$ vertės jų plaukuose padidėjo. Šis poveikis buvo pastebimas jau pirmaisiais kormoranų ekspansijos į naujas teritorijas metais.
4. Juodkrantės kormoranų kolonijoje didžiausio paukščių aktyvumo zonose K ir Cu koncentracija geltonkaklių pelių audiniuose buvo padidėjusi, o Rb ir Pb sumažėjusi.
5. Žvėrių stebėjimo kameromis Juodkrantės ir Lukšto kormoranų kolonijose buvo registruoti vienuolikos (tarp jų trijų nevietinių) rūšių žinduoliai. Kolonijoje lapių (*Vulpes vulpes*) ir mangutų (*Nyctereutes procyonoides*) aktyvumas kormoranų perėjimo sezono metu buvo kelis kartus didesnis nei kitu laiku. Kormoranams perint mangutų, lapių ir šernų (*Sus scrofa*) paros aktyvumas keitėsi, stirnų (*Capreolus capreolus*) paros aktyvumas išliko nepakitęs.

MOKSLINĖ IR PRAKTINĖ REIKŠMĖ

Žinduolių tyrimų didžiųjų kormoranų kolonijose stoka parodė, kad šių paukščių vaidmuo ekosistemose nebuvo nuodugniai įvertintas. Šio tyrimo rezultatai leidžia geriau apibūdinti kormoranų poveikio aplinkai kompleksiškumą. Pirmą kartą išaiškinta kolonijos dydžio reikšmė ir nustatyta, kad didesnėje kolonijoje paukščių įtaka smulkiesiems žinduoliams yra neigiama. Įrodyta, kad kolonijos poveikis pasireiškia jau pirmaisiais metais po jos susiformavimo. Patvirtinta, kad maisto medžiagų pernešimo į sausumos ekosistemas įtaka yra netiesioginė, ji priklauso nuo paukščių išmatų biologinės taršos poveikio graužikų maisto objektams.

Didžiųjų kormoranų kolonijos poveikio greičio įvertinimas turi praktinę reikšmę. Jis parodo, kad paukščių išbaidymas iš užimamų teritorijų iki perėjimo gali turėti neigiamas pasekmes. Pradedant kormoranus baidyti per anksti, jų kolonijos fragmentuojasi ir paukščiai išplinta ir suka lizdus naujose buveinėse. Susidariusios kolonijos jau pirmaisiais metais pakeičia ekosistemą. Perinčių kormoranų baidymas nuo lizdų ribojant išsiritusių kiaušinių skaičių, yra naudingesnė priemonė už paukščių gąsdinimą iki perėjimo sezono pradžios. Lietuvoje kormoranų gausos reguliavimo darbai yra atliekami, jeigu kolonijoje yra daugiau, kaip 100 perinčių porų. Mūsų tyrimų rezultatai rodo, kad kormoranų kolonijos neviršijančios 200 perinčių porų nedaro neigiamo poveikio jose aptinkamiems žinduoliams.

REFERENCES

1. Adamonytė, G., Iršėnaitė, R., Motiejūnaitė, J., Taraškevičius, R., Matulevičiūtė, D., 2012. Myxomycetes in a forest affected by great cormorant colony: a case study in Western Lithuania. Fungal Diversity 13 (1), 131–146.
2. Akbaba, B., Ayas, Z., 2012. Camera trap study on inventory and daily activity patterns of large mammals in a mixed forest in north-western Turkey. Mammalia 76 (1), 43–48.
3. Alcantara, M., Diaz, M., 1996. Patterns of body weight, body size, and body condition in the wood mouse *Apodemus sylvaticus* L.: effects of sex and habitat quality. Proceedings of the European Congress of Mammalogy I; 18–23 March 1991; Lisbon, Portugal. Lisbon, Portugal: Museu Bocage, 141–149.
4. Alejūnas, P., Stirkė, V., 2010. Small mammals in northern Lithuania: species diversity and abundance. Ekologija 56 (3–4), 110–115.
5. Anderson, W.B., Polis, G.A., 1999. Nutrient fluxes from water to land: seabirds affect plant nutrient status on Gulf of California islands. Oecologia 118 (3), 324–332.
6. Andras, P., Krizani, I., Stanko, M., 2006. Free-living rodents as monitors of environmental contaminants at a polluted mining dump area. Carpathian Journal of Earth and Environmental Sciences 1 (2), 51–62.
7. Ayers, C.R., Hanson-Dorr, K.C., O'Dell, S., Lovel, C.D., Jones, M.L., 2015. Impacts of colonial waterbirds on vegetation and potential restoration of island habitats. Restoration Ecology 23 (3), 252–260.
8. Balčiauskas, L., 2004. Methods of investigation of terrestrial ecosystems. Part I. Animal surveys. Vilnius (VUL), 183.
9. Balčiauskas, L., Alejūnas, P., 2011. Small mammal species diversity and abundance in Žagarė Regional Park. Acta Zoologica Lituanica 21 (2), 163–172.
10. Balčiauskas, L., Balčiauskienė, L., Janonytė, A., 2012. Reproduction of the root vole (*Microtus oeconomus*) at the edge of its distribution range. Turkish Journal of Zoology 36 (5), 668–675.
11. Balčiauskienė, L., Balčiauskas, L., Čepukienė, A., 2009. Demographic and morphometric parameters of the yellow-necked

mouse (*Apodemus flavicollis*) in late autumn-early spring in Lithuania. Acta Biologica Universitatis Daugavpiliensis 9 (1), 25–34.

12. Bobek, B., 1969. Survival, turnover and production of small rodents in a beech forest. Acta Theriologica 15, 191–210.
13. Bogdziewicz, M., Zwolak, R., 2014. Responses of small mammals to clear-cutting in temperate and boreal forests of Europe: a meta-analysis and review. European Journal of Forest Research 133 (1), 1–11.
14. Bostrom, M.K., Ostman, O., Bergenius, M.A.J., Lunneryd, S.G., 2012. Cormorant diet in relation to temporal changes in fish communities. ICES Journal of Marine Science 69 (2), 175 –183.
15. Bregnballe, T., 1996. Development of the north and central European population of cormorant *Phalacrocorax carbo sinensis*, 1960–1995. Dansk Ornitologisk Forenings Tidsskrift 90, 15–20.
16. Bregnballe, T., Volponi, S., Eerden, M.R., Rijn, S., Lorentzen, S.H., 2011. Status of the breeding population of great Cormorants *Phalacrocorax carbo* in the Western palearctic in 2006. Proceedings 7th International Conference on Cormorants, Villeneuve, Switzerland November 2005.
17. Briani, D.C., Palma, A.R.T., Vieira, E.M., Henriques, R.P.B., 2004. Post-fire succession of small mammals in the Cerrado of central Brazil. Biodiversity and Conservation 13 (5), 1023–1037.
18. Bryja, J., Heroldova, M., Zejda, J., 2002. Effects of deforestation on structure and diversity of small mammal communities in the Moravskoslezské Beskydy Mts (Czech Republic). Acta Theriologica 47 (3), 295–306.
19. Bush, E.R., Buesching, C.D., Slade, E.M., Macdonald, D.W., 2012. Woodland recovery after suppression of deer: cascade effects for small mammals, wood mice (*Apodemus sylvaticus*) and bank voles (*Myodes glareolus*). PLoS ONE 7, e31404.
20. Carey, A.B., Harrington, C.A., 2001. Small mammals in young forests: implications for management for sustainability. Forest Ecology and Management 154 (1–2), 289–309.
21. Craig, E.C., Elbin, S.B., Danoff-Burg, J.A., Palmer, M.I., 2012. Impacts of Double-Crested Cormorants (*Phalacrocorax auritus*) and Other Colonial Waterbirds on Plant and Arthropod Communities on Islands in an Urban Estuary. Waterbirds 35 (1), 4–12.

22. Čepukienė, A., Jasiulionis, M., 2012. Small mammal community changes during forest succession (Pakruojis district, north Lithuania). Zoology and Ecology 22 (3–4), 144–149.
23. Dagys, M., Zarankaitė, J., 2013. Status of the breeding population of Great Cormorants in Lithuania in 2012. – In: Bregnballe, T., Lynch, J., Parz-Gollner, R., Marion, L., Volponi, S., Paquet, J-Y. & van Eerden, M.R. (eds.) 2013. National reports from the 2012 breeding census of Great Cormorants *Phalacrocorax carbo* in parts of the Western Palearctic. IUCN-Wetlands International Cormorant Research Group Report. Technical Report from DCE – Danish Centre for Environment and Energy, Aarhus University 22, 69–71.
24. Diaz-Ruiz, F., Caro, J., Delibes-Mateos, M., Arroyo, B., Ferreras, P., 2015. Drivers of red fox (*Vulpes vulpes*) daily activity: prey availability, human disturbance or habitat structure? Journal of Zoology 298 (2), 128–138.
25. Domínguez, M., Gutiérrez, E., González-Domínguez, B., Román-Écija, M., Avila, J., Ramo, C., Gonzalez, J., García, L., 2016. Impacts of protected colonial birds on soil microbial communities: When protection leads to degradation. Soil Biology and Biochemistry 105, 59–70.
26. Eerden, M.R., Gregersen, J., 1995. Long-term changes in the north west European population of cormorants *Phalacrocorax carbo sinensis*. Ardea 83, 61–79.
27. Ellis, J.C., Farina, J.M., Witman, J.D., 2006. Nutrient transfer from sea to land: the case of gulls and cormorants in the Gulf of Maine. Journal of Animal Ecology 75 (2), 565–574.
28. Fisher, J.T., Wilkinson, L., 2005. The response of mammals to forest fire and timber harvest in North American boreal forest. Mammal Review 35 (1), 51–81.
29. Fox, B.J., 1995. Long-term studies of small mammal communities from disturbed habitats in eastern Australia. Academic Press, Orlando, Florida, USA, 467–501.
30. Fritsch, C., Cosson, R.P., Coeurdassier, M., Raoul, F., Giraudoux, P., Crini, N., Vaufleury, A., Scheifler, R., 2010. Responses of wild small mammals to a pollution gradient: Host factors influence metal and metallothionein levels. Environmental Pollution 158 (3), 827–840.
31. Garcia, L.V., Ramo, C., Aponte, C., Moreno, A., Dominguez, M.T., Gomez-Aparicio, L., Redondo, R., Maranon, T., 2011. Protected

wading bird species threaten relict centenarian cork oaks in a Mediterranean biosphere reserve: a conservation management conflict. Biological Conservation 144 (2), 764–771.

32. Goc, M., Iliszko, L., Stempniewicz, L., 2005. The largest European colony of great cormorant on the Vistula spit (N Poland) an impact of the forest ecosystem. Ecological Questions 6, 93–103.
33. Gosalbez, J., Castian, E., 1995. Reproductive cycle, abundance and population structure of *Apodemus flavicollis* (Melchior, 1834) in the western Pyrenees. Mammalia 59 (3), 385–396.
34. Grabham, A.A., Ventress, G., Hayward, M.W, 2019. The diet of denning female European pine martens (*Martes martes*) in Galloway Forest District, South West Scotland, Great Britain. Mammal Research 64 (5), 87–97.
35. Gražulevičius, G., Elertas, D., 2005. Didysis kormoranas Kuršių nerijoje [Great Cormorant in Curonian Lagoon]. Žurnalas apie gamtą, 5 (11), 8–10.
36. Gremillet, D., Schmid, D., Culik, B., 1995. Energy requirements of breeding great cormorants *Phalacrocorax carbo sinensis*. Marine Ecology Progress Series 121 (1–3), 1–9.
37. Gryz, J., Krauze-Gryz, D., 2019. Changes in the tawny owl *Strix aluco* diet along an urbanisation gradient. Biologia 74, 279–285
38. Gwiazda, R., Jarocha, K., Szrek-Gwiazda, E., 2010. Impact of a small cormorant (*Phalacrocorax carbo sinensis*) roost on nutrients and phytoplankton assemblages in the littoral regions of a submontane reservoir. Biologia 65 (4), 742–748.
39. Herrmann, C., 2019. Population Development of Baltic Bird Species: Great Cormorant (*Phalacrocorax carbo sinensis*). HELCOM Baltic Sea Environment Fact Sheet 2018, Published 20.5.2019.
40. Hobara, S., Osono, T., Koba, K., Tokuchi, N., Fujiwara, S., Kameda, K., 2001. Forest floor quality and N transformations in a temperate forest affected by avian-derived N deposition. Water, Air, & Soil Pollution 130 (1), 679–684.
41. Hobara, S., Koba, K., Osono, T., Tokuchi, N., Ishida, A., Kameda, K., 2005. Nitrogen and phosphorus enrichment and balance in forests colonized by cormorants: Implications of the influence of soil adsorption. Plant and Soil 268, 89–101.
42. Hopton, M.E., Cameron, G.N., Cramer, M.J., Polak, M., Uetz, G.W., 2009. Live animal radiography to measure developmental instability

in populations of small mammals after a natural disaster. Ecological Indicators 9 (5), 883–891.

43. Hoyo, J., Elliott, A., Sargatal, J., 1992. Handbook of the Birds of the World. Ostrich to Ducks, Lynx 1, 326–353.
44. Ikeda, T., Uchida, K., Matsuura, Y., Takahashi, H., Yoshida, T., Kaji, K., Koizumi, I., 2016. Seasonal and Diel Activity Patterns of Eight Sympatric Mammals in Northern Japan Revealed by an Intensive Camera-Trap Survey. PLoS ONE 11, e0163602.
45. Ishida, A., 1996. Changes of soil properties in the colonies of the common cormorant, *Phalacrocorax carbo*. Journal of Forestry Research 1, 31–35.
46. Ishizuka, K., 1966. Ecology of the ornithocoprophilous plant communities on breeding places of the black-tailed gull, *Larus crassirostris*, along the coast of Japan. Ecological Review 16, 229–244.
47. Jasiulionis, M., Čepukienė, A., Balčiauskas, L., 2011. Small mammal community changes during succession of the planted forest. Acta Zoologica Lituanica 22 (4), 293–300.
48. Jedrzejewski, W., Jedrzejewska, B., 1992. Foraging and diet of the red fox *Vulpes vulpes* in relation to variable food resources in Biatowieza National Park, Poland. Ecography 15 (2), 212–220.
49. Jones, C.G., Lowton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. Oikos 69 (3), 373–386.
50. Julliard, R., 2000. Sex-specific dispersal in spatially varying environments leads to habitat-dependent evolutionary stable offspring sex ratios. Behavioral Ecology 11 (4), 421–428.
51. Juškaitis, R., Ulevičius, A., 2002. Small mammals of the Curonian Spit National Park. Theriologia Lituanica 2, 34–46.
52. Juškaitis, R., Uselis, V., 2005. Small mammals of the Viešvilė Strict Nature Reserve. Theriologia Lituanica 5, 40–50.
53. Kameda, K., Koba, K., Hobara, S., Osono, T., Terai, M., 2006. Pattern of natural 15N abundance in lakeside forest ecosystem affected by cormorant-derived nitrogen. Hydrobiologia 567 (1), 69–86.
54. Klimaszyk, P., Brzeg, A., Rzymski, P., Piotrowicz, R., 2015. Black spots for aquatic and terrestrial ecosystems: impact of a perennial cormorant colony on the environment. Science of the Total Environment 517, 222–231.

55. Klimaszyk, P., Joniak, T., 2011. Impact of black cormorant (*Phalacrocorax carbo sinensis* L.) on the transport of dissolved organic carbon from the catchment area to the lakes. Polish Journal of Soil Science 42 (2), 161–166.
56. Klimaszyk, P., Joniak, T., Rzymski, P., 2014. Roosting colony of cormorants (*Phalacrocorax carbo sinensis* L.) as a source of nutrients for the lake. Limnological Review 14 (3), 111–119.
57. Klimaszyk, P., Rzymsky, P., 2016. The complexity of ecological impacts induced by great cormorants. Hydrobiologia 771 (1), 13–30.
58. Knyva, V., Rumbutis, S., 2016. Didžiųjų kormoranų populiacijos gausos reguliavimo programos priemonių įgyvendinimas 2015–2016 metais. Ataskaita, 1–64.
59. Kohl, F., 2015. How many Cormorants in Europe? Great cormorant *Phalacrocorax carbo* in Europe. Population Development 1970–2014. A Documentation of EAA - European Anglers Alliance.
60. Kohno, H., Ota, H., 1991. Reptiles in a seabird colony: herpetofauna of Nakanokamiishima Island of the yaeyama group, Ryukyu Archipelago. Island Studies in Okinawa 9, 73–89.
61. Kolb, G.S., Palmborg, C., Taylor, A.R., Baath, E., Hamback, A.P., 2015. Effects of nesting cormorants (*Phalacrocorax carbo*) on soil chemistry, microbial communities and soil fauna. Ecosystems 18 (4), 643–657.
62. Koskela, E., Jonsson, P., Hartikainen, T., Mappes, T., 1998. Limitation of reproductive success by food availability and litter size in the bank vole, *Clethrionomys glareolus*. Proceedings of the Royal Society 265, 1129–1134.
63. Kozakiewicz, M., Kozakiewicz, A., 2008. Long-term dynamics and biodiversity changes in small mammal communities in a mosaic of agricultural and forest habitats. Annales Zoologici Fennici 45 (4), 263–269.
64. Krebs, C.J., 1999. Ecological methodology. 2nd ed. Vancouver (Benjamin Cummings), 624.
65. Kuiken, T., Leighton, F. A., Wobeser, G., Wagner, B., 1999. Causes of morbidity and mortality and their effect on reproductive success in double-crested cormorants from Saskatchewan. Journal of Wildlife Diseases 35 (2), 331–346.
66. Kutorga, E., Iršėnaitė, R., Iznova, T., Kasparavičius, J., Markovskaja, S., Motiejūnaitė, J., 2013. Species diversity and

composition of fungal communities in a Scots pine forest affected by the great cormorant colony. Acta Mycologica 48 (2), 173–188.

67. Lafferty, D.J.R., Hanson-Dorr, K.C., Prisock, A.M., Dorr, B.S., 2016. Biotic and abiotic impacts of Double-crested cormorant breeding colonies on forested islands in the southeastern United States. Forest Ecology and Management 69, 10–19.
68. Lindeboom, H.J., 1984. The nitrogen pathway in a penguin rookery. Ecology 65 (1), 269–277.
69. Lindell, L., Mellin, M., Musil, P., Przybysz, J., Zimmermann, H., 1995. Status and population development of breeding Cormorants *Phalacrocorax carbo sinensis* in central Europe. Ardea 83 (1), 81–92.
70. Maesako, Y., 1999. Impacts of streaked shearwater (*Calonectris leucomelas*) on tree seedling regeneration in a warm-temperate evergreen forest on Kanmurijima Island, Japan. Plant Ecology 145, 183–190.
71. Malecha, A. W., Antczak, M., 2013. Diet of the European polecat *Mustela putorius* in an agricultural area in Poland. Folia Zoologica 62 (1), 48–53.
72. Martiniaková, M., Omelka, R., Grosskopf, B., Duranova, H., Stawarz, R., Balaz, I., 2015. Further investigation of risk elements content in the bones of wild rodents from a polluted area in Slovakia. Acta Veterinaria Scandinavica 57 (1), 46.
73. Martiniaková, M., Omelka, R., Grosskopf, B., Jancova, A., 2010. Yellow-necked mice (*Apodemus flavicollis*) and bank voles (*Myodes glareolus*) as zoomonitors of environmental contamination at a polluted area in Slovakia. Acta Veterinaria Scandinavica 52 (1), 58.
74. Masi, S., Cipolletta, C., Robbins, M., 2009. Western Lowland Gorillas (*Gorilla gorilla gorilla*) Change Their Activity Patterns in Response to Frugivory. American Journal of Primatology 71 (2), 91–100.
75. Matulevičiūtė, D., Motiejūnaitė, J., Uogintas, D., Taraškevičius, R., Dagys, M., Rašomavičius, V., 2018. Decline of a protected coastal pine forest under impact of a colony of great cormorants and the rate of vegetation change under ornithogenic influence. Silva Fennica 52 (2), 7699.
76. Mažeikytė, R., 2002. Small mammals of the Kanio Raistas Botanical-Zoological Reserve. Theriologia Lituanica 2, 58–69.

77. Millus, S.A., Stapp, P., 2008. Interactions between seabirds and endemic deer mouse populations on Santa Barbara Island, California. Canadian Journal of Zoology 86 (9), 1031–1041.
78. Misztal-Szkudlinska, M., Szefer, P., Konieczka, P., Namiesnik J., 2011. Biomagnification of mercury in trophic relation of Great Cormorant (*Phalacrocorax carbo*) and fish in the Vistula Lagoon, Poland. Environmental Monitoring and Assessment 176 (1–4), 439–449.
79. Moors, P.J., 1985. Norway rats (*Rattus norvegicus*) on the Noises and Motukawao islands, Hauraki Gulf, New Zealand. New Zealand Journal of Ecology 8, 37–54.
80. Motiejūnaitė, J., Iršėnaitė, R., Adamonytė, G., Dagys, M., Taraškevičius, R., Matulevičiūtė, D., Koreivienė, J., 2014. Pine forest lichens under eutrophication generated by a great cormorant colony. Lichenologist 46 (2), 213–228.
81. Myllymaki, A., 1977: Demographic mechanisms in the fluctuating populations of the field vole *Microtus agrestis.* Oikos 29 (3), 468–493.
82. Nadelhoffer, K.J., Fry, B., 1988. Controls on natural nitrogen-15 and carbon-13 abundances in forest soil organic matter. Soil Science Society of America Journal 52 (6), 1633–1640.
83. Nakagawa, M., Hyodo, F., Nakashizuka, T., 2007. Effect of forest use on trophic levels of small mammals: An analysis using stable isotopes. Canadian Journal of Zoology, 85 (4), 472–478.
84. Nelson, J. B., 2005. Pelicans, Cormorants and their relatives. Oxford: Oxford University Press, 662.
85. Niethammer, J., Krapp, F., 1978. Handbuch der Säugetiere Europas, Vol. I. Akademische Verlagsgesellschaft. Wiesbaden, 1–476.
86. Nunes, A.C., Auffray, J.C., Mathias, M.L., 2001. Developmental instability in a riparian population of the Algerian mouse (*Mus spretus*) associated with a heavy metal-polluted area in Central Portugal. Archives of Environmental Contamination and Toxicology 41 (4), 515–521.
87. Nyholm, N.E.I., Tyler, G., 2000. Rubidium content of plants, fungi and animals closely reflects potassium and acidity conditions of forest soils. Forest Ecology and Management 134 (1), 89–96.
88. Oleksyk, T.K., Novak, J.M., Purdue, J.R., Gashchak, S.P., Smith, M.H., 2004. High levels of fluctuating asymmetry in populations of

Apodemus flavicollis from the most contaminated areas in Chornobyl. Journal of Environmental Radioactivity 73 (1), 1–20.

89. Olenev, G.V., Grigorkina, E.B., 2011. Dynamics of Sex Ratio in Populations of Cyclomorphic Mammals (Rodentia, Cricetidae, Muridae). Biology Bulletin 38 (8), 797–808.
90. Otero, X.L., Tejada, O., Martin-Pastor, M., Pena, S., Ferreira, T.O., Perez-Alberti, A., 2015. Phosphorus in seagull colonies and the effect on the habitats. The case of yellow-legged gulls (*Larus michahellis*) in the Atlantic Islands National Park (Galicia-NW Spain). Science of the Total Environment 532, 383–397.
91. Pearce, J., Venier, L., 2005. Small mammals as bioindicators of sustainable boreal forest management. Forest Ecology and Management 208 (1–3), 153–175.
92. Polis, G.A., Hurd, S.D., 1996. Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. American Naturalist 147 (3), 396–423.
93. Prūsaitė, J. (comp.) 1988. Lithuanian Fauna. Mammals. Vilnius: Mokslas, 1–293.
94. Pūtys, Ž., 2012. Great Cormorant *Phalacrocorax carbo Sinensis* Diet and its effect on fish community in the eutrophic curonian lagoon ecosystem. Summary of doctoral dissertation. VUL, Vilnius, 1–48.
95. Riddick, S.N., Dragosits, U., Blackall, T.D., Daunt, F., Wanless, S., Sutton, M.A., 2012. The global distribution of ammonia emissions from seabird colonies. Atmospheric Environment 55, 319–327.
96. Ryan, C.P., Anderson, W.G., Gardiner, L.E., Hare, J.F., 2012. Stress-induced sex ratios in ground squirrels: support for a mechanistic hypothesis. Behavioral Ecology 23 (1), 160–167.
97. Rosenfeld, C.S., Grimm, K.M., Livingston, K.A., Brokman, A.M., Lamberson, W.E., Roberts, R.M., 2003. Striking variation in the sex ratio of pups born to mice according to whether maternal diet is high in fat or carbohydrate. Proceedings of the National Academy of Sciences of the United States of America 100 (8), 4628–4632.
98. Stanevičius, V., Paltanavičius, S., 1997. The Cormorant *Phalacrocorax carbo* in southern and eastern Lithuania. Ekologia polska, XLV (1), 123–124.

99. Steffens, W., 2010. Great cormorant – substantial danger to fish populations and fishery in Europe. Bulgarian Journal of Agricultural Science 16 (3), 322–331.

100. Taraškevičius, R., Motiejūnaitė, J., Zinkutė, R., 2013. Pedogeochemical anomalies in surroundings of great cormorant colony (case study in Lithuania). E3S Web of Conferences.

101. Tête, N., Fritsch, C., Afonso, E., Coeurdassier, M., Lambert, J.C., Giraudoux, P., Scheifler, R., 2013. Can body condition and somatic indices be used to evaluate metal-induced stress in wild small mammals? PLoS ONE 8: e66399.

102. Velickovic, M., 2007. Measures of the developmental stability, body size and body condition in the black-striped mouse (*Apodemus agrarius*) as indicators of a disturbed environment in northern Serbia. Belgian Journal of Zoology 137 (2), 147–156.

103. Veum, L.M., Dorr, B.S., Hanson-Dorr, K.C., Moore, J.R., Rush, S.A., 2019. Double-crested cormorant colony effects on soil chemistry, vegetation structure and avian diversity. Forest Ecology and Management 453, 1047264.

104. White, C.R., Boertmann, D., Gremillet, D., Butler, P.J., Green J.A., Martin G.R., 2011. The relationship between sea surface temperature and population growth of Great Cormorants near Disco Bay, Greenland. Ibis 153 (1), 170–174.

105. Wiebold J.L., Stanfield P.H., Becker W.C. Hillers J. K., 1986. The effect of restraint stress in early pregnancy in mice. Journal of reproduction and fertility 78 (1): 185–192.

106. Wilson, D.E., Lacher, T.E., Mittermeier, R.A. 2017. Handbook of the mammals of the world Vol. 7 (Rodents II). Lynx Edicions, Barselona, 1–1008.

107. Zolkos, K., Kukwa, M., Afranowicz-Cieślak, R., 2013. Changes in the epiphytic lichen biota in the Scots pine (*Pinus sylvestris*) stands affected by a colony of grey heron (*Ardea cinerea*): a case study from northern Poland. Lichenologist 45 (6), 815–823.

108. Zoller, H., Drygala, F., 2013. Activity patterns of the invasive raccoon dog (*Nyctereutes procyonoides*) in North East Germany. Folia Zoologica 62 (4), 290–296.

LIST OF PUBLICATIONS ON THE DISERTATION TOPIC

The dissertation is based on the following co-authored original publications in journals with an impact factor and referred in the Clarivate Analysis Web of Science database. Throughout the text, the publications are referred using the Roman numerals:

I. Balčiauskienė, L., **Jasiulionis, M.**, Balčiauskas, L., 2014. Loss of diversity in a small mammal community in a habitat influenced by a colony of great cormorants. Acta Zoologica Bulgarica 66 (2), 229–234. (Animal Science and Zoology Q3; Ecology, Evolution, Behavior and Systematics Q4)

II. Balčiauskas, L., Balčiauskienė, L., **Jasiulionis, M.,** 2015. Mammals under a colony of great cormorants: population structure and body condition of yellow-necked mice. Turkish Journal of Zoology 39 (5), 941–948. doi: 10.3906/zoo-1407-27 (Animal Science and Zoology Q3)

III. Balčiauskienė, L., Balčiauskas, L., **Jasiulionis, M**., 2015. Skull variability of mice and voles inhabiting the territory of a great cormorant colony. Biologia 70 (10), 1406–1414. doi: 10.1515/biolog-2015-0152 (Animal Science and Zoology Q3; Ecology, Evolution, Behavior and Systematics Q3)

IV. Balčiauskas, L., Skipitytė, R., **Jasiulionis, M.**, Trakimas, G., Balčiauskienė, L., Remeikis, V., 2016. The impact of Great Cormorants on biogenic pollution of land ecosystems: Stable isotope signatures in small mammals. Science of the Total Environment 565, 376–383. doi: 10.1016/j.scitotenv.2016.04.185 (Environmental Chemistry Q1)

V. Balčiauskas, L., Skipitytė, R., **Jasiulionis, M**., Balčiauskienė, L., Remeikis, V., 2018. Immediate increase in isotopic enrichment in small mammals following the expansion of a great cormorant colony. Biogeosciences 15 (2), 3883–3891. doi: 10.5194/bg-15-3883-2018 (Ecology, Evolution, Behavior and Systematics Q1)

VI. **Jasiulionis, M**., Balčiauskas, L., Balčiauskienė, L., Taraškevičius, R., 2018. Accumulation of chemical elements in yellow-necked mice under a colony of great cormorants. Chemosphere. 213, 156–163. doi: org/10.1016/j.chemosphere.2018.09.025 (Environmental Chemistry Q1)

VII. Balčiauskas, L., Skipitytė, R., Balčiauskienė, L., **Jasiulionis, M.,** 2019. Resource partitioning confirmed by isotopic signatures allows small mammals to share seasonally flooded meadows. Ecology and Evolution 9 (9), 5479–5489. doi: 10.1002/ece3.5144 (Ecology Q2)

VIII. **Jasiulionis M**., Balčiauskas, L., 2020. Seasonal and daily activity patterns of mammals in the colony of cormorants. (*Unpublished manuscript*)

AUTHOR CONTRIBUTIONS IN THE CORRESPONDING PAPERS

In dissertation publications, research on impact of the colonies of great cormorants on mammals was done by M. Jasiulionis and co-authors. Contribution of co-authors in each study was as described below.

I. Conceptualization: LaB, **MJ** and LiB. Fieldwork: **MJ**. Dissection: LiB, LaB and **MJ**. Data analysis: LiB. Paper writing: LaB and **MJ.** All authors approved the final manuscript.

II. Conceptualization: LiB**, MJ** and LaB. Fieldwork: **MJ**. Dissection: LiB, LaB and **MJ**. Paper writing: LiB, LaB and **MJ.** All authors approved the final manuscript.

III. Conceptualization: LaB. Fieldwork: **MJ**. Morphometry measurements: LaB. Dissection: LiB, LaB. Paper writing: LaB, LiB. All authors approved the final manuscript.

IV. Conceptualization: GT. Fieldwork: **MJ**, LiB, LaB. Dissection: LiB and LaB. Stable isotope analysis: RS, **MJ**, VR. Data analysis: RS, LiB, **MJ**. Paper writing: LiB, **MJ**, RS. All authors approved the final manuscript.

V. Conceptualization: LiB. Fieldwork: **MJ**, LiB, LaB. Dissection: LiB, **MJ** and LaB. Stable isotope analysis: RS, **MJ**, VR. Data analysis: RS, LiB. Paper writing: LiB, RS, LaB. All authors approved the final manuscript.

VI. Conceptualization: **MJ**. Fieldwork: **MJ**, LiB and LaB. Dissection: LiB, **MJ** and LaB. Chemical analysis: **MJ**, RT. Data analysis: **MJ**, RT, LiB, LaB. Paper writing: **MJ** and LiB. All authors approved the final manuscript.

VII. Conceptualization: LiB. Fieldwork: LiB, LaB, **MJ**. Stable isotope analysis: RS and **MJ**. Data analysis: RT, LiB, LaB, **MJ**. Paper writing: LiB, RS and LaB. All authors approved the final manuscript.

VIII. Conception and design: **MJ** and LiB. Fieldworks and data analysis **MJ**. Paper writing: **MJ** and LiB. Both authors approved the final manuscript.

LIST OF CONFERENCE PRESENTATIONS ON THE SUBJECT OF THE DISSERTATION

1. **Jasiulionis, M.,** Balčiauskienė, L., Balčiauskas, L., 2013. Didžiųjų kormoranų (*Phalacrocorax carbo*) kolonijos poveikis smulkiųjų žinduolių bendrijai. *7-oji nacionalinė jūros mokslų ir technologijų konferencija Jūros ir krantų tyrimai – 2013*. Klaipėda, Lithuania.
2. Balčiauskienė, L. **Jasiulionis, M.,** Balčiauskas, L., 2013. Small mammals in the biggest colony of Great Cormorant in Lithuania. *VII International Conference „Research and conservation of biological diversity in Baltic Region“*. Daugavpils, Latvia.
3. Balčiauskienė, L., **Jasiulionis, M.,** Balčiauskas, L., 2014. Under an onslaught of faeces: Small mammals in a colony of Great Cormorants. *88th Annual Meeting of the German Society for Mammalian Biology*. Giessen, Germany.
4. Mažeika, V., Navickaitė, D., **Jasiulionis, M.,** Balčiauskienė, L., 2014. Helminths of yellow-necked mouse (*Apodemus flavicollis*) trapped in the territory of colony of Great Cormorants. *9th Baltic Theriological Conference*. Daugavpils, Latvia.
5. **Jasiulionis, M**., Balčiauskienė, L., Balčiauskas, L., 2014. Mammal community in a habitat influenced by a colony of great cormorant. *9th Baltic Theriological Conference.* Daugavpils, Latvia.
6. Mažeika, V., Navickaitė, D., **Jasiulionis, M**., Balčiauskienė, L., 2015. An investigation on helminths of yellow-necked mouse (*Apodemus flavicollis*) and bank vole (*Myodes glareolus*) from the colony of Great Cormorants in Juodkrantė. *8th International conference on biodiversity research*. Daugavpils, Latvia.
7. **Jasiulionis, M**., Taraškevičius R., Balčiauskienė, L., Balčiauskas, L., Alejūnas, P., 2015. Introductory study of accumulation of chemical elements in yellow-necked mice and bank voles in the territory of great cormorant colony. *8th International conference on biodiversity research*. Daugavpils, Latvia.
8. **Jasiulionis, M**., Skipitytė R., Balčiauskienė, L., Trakimas, G., Balčiauskas, L., Remeikis, V., 2015. Stabile isotope signatures in small mammals living in the colonies of great cormorants. *8th International conference on biodiversity research*. Daugavpils, Latvia.

9. Taraškevičius, R., Čičiurkaitė, I., Garnaga-Budrė, G., **Jasiulionis, M**., Lesutienė, J., Montvydienė, D., Suzdalev, S., Vaitkevičienė, V., 2018. Spektrometro SPECTRO XEPOS HE galimybės aplinkos mėginių cheminės sudėties tyrimuose. *11-oji nacionalinė jūros mokslų ir technologijų konferencija „Jūros ir krantų tyrimai 2018“*. Klaipėda, Lithuania.
10. Balčiauskas, L., **Jasiulionis, M**., Balčiauskienė, L., Skipitytė., R., 2019. Living on the tough side: mammals in the great cormorant colonies. *11th International Symposium of Integrative Zoology*. Albany, Auckland, New Zealand.
11. **Jasiulionis, M**., Balčiauskienė, L., Balčiauskas, L., 2019. Living under a rain of faeces: mammals in the colony of cormorants. *62nd international conference for students of physics and natural sciences. OPEN READINGS 2019*. Vilnius, Lithuania.
12. **Jasiulionis, M**., Balčiauskas, L., 2019. Seasonal and daily activity of mammals in the colony of cormorants. *3rd International Conference on Life and Environmental Sciences "Smart Bio“*. Kaunas, Lithuania.

AWARDS

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ADDITIONAL PAPER PUBLISHED DURING THE PHD STUDIES (NOT INCLUDED IN THE THESIS)

Publication in journal with an impact factor and referred in the Clarivate Analysis Web of Science database.

Simanavičius, M., Juškaitė, K., Verbickaitė, A., **Jasiulionis, M.,** Tamošiūnas, P.L., Petraitytė-Burneikienė, R., Žvirblienė, A., Ulrich, R.G., Kučinskaitė-Kodzė, I., 2018. Detection of rat hepatitis E virus, but not human pathogenic hepatitis E virus genotype 1–4 infections in wild rats from Lithuania. Veterinary Microbiology 221, 129–133. doi: 10.1016/j.vetmic.2018.06.014 (Medicine Q1)

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Research Grants:
Colony of Great Cormorants in forest ecosystem – hypertrophication effect and rates of dynamics, 2012–2014 (LEK-3/2012).
Development of new diagnostic tools for hepatitis E virus (HEV) and studies on HEV prevalence in Lithuania 2015–2018 (MIP-039/2015).

COPIES OF PUBLICATIONS

PAPER I

Loss of diversity in a small mammal community in a habitat influenced by a colony of great cormorants

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Bulgarian Academy of Sciences publication

Terrestrial Ecology and Behaviour
Research Article

ACTA ZOOLOGICA BULGARICA
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Loss of Diversity in a Small Mammal Community in a Habitat Influenced by a Colony of Great Cormorants

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Abstract: The diversity and relative abundance of small mammals was studied in the territory occupied by the largest colony of breeding great cormorants (*Phalacrocorax carbo sinensis*) in Lithuania. The area of 13.6 ha with over 3800 cormorant nests, is situated in the Curonian Spit National Park in West Lithuania. The aim of the study was to test if the small mammal community is influenced by the presence of the colony. We found that in general the diversity of small mammals in the area was low. The community was dominated by yellow-necked mice (73.1% of all trapped individuals), with bank voles subdominant (22.2%). The proportion of five other species trapped in the territory of the colony and its edge was in the range of 0.6–1.6%. The zones of colony expansion (where influence of the colony is just started) and established active colony (long term influence) were found to have most negative impact on the small mammal community (only 3–4 species present, Shannon's H = 0.55–1.10). Only two species were registered in the edge of these zones. The relative abundance of small mammals was lower in the territory of active zones of influence. In zones of the former influence of the colony, however, the abundance was higher, than in the zones of recent influence.

Keywords: *Phalacrocorax carbo sinensis*; colony influence; voles and mice

Introduction

The continental subspecies of great cormorant (*Phalacrocorax carbo sinensis*) forms breeding colonies near inland water bodies and along the shores of lagoons, with the largest colonies in Europe containing up to 12-14 thousand breeding pairs (Kirikova *et al.* 2007, Nemtzov 2008, Herrmann *et al.* 2012). Cormorants were eradicated from the Baltic Sea region in 19th century, but returned and started breeding again in 1938 (Ivanauskas 1938; Samusenko 2008, Herrmann *et al.* 2012). By 2009, approximately 165,000 pairs of great cormorants bred in the basin of the Baltic Sea. In recent years, the population of the southern part of the Baltic has been stable, whilst in central and northern parts it has been increasing (Herrmann *et al.* 2012).

The cormorant colony on the Curonian Spit of Lithuania established itself in the 19th century, was eradicated around 1887 (Gražulevičius, Elertas 2005) and once again re-established in1989 (Stanevičius, Paltanavičius 1997). The number of breeding pairs reached 2700 by 2003, stabilized at about 3000 from 2005 to 2010, then peaked at 3808 in 2011 (Ložys, Dagys 2008, Putys 2012). In 2011, the cormorant colony covered an area of 12.0 ha.

This remains the largest cormorant colony in Lithuania, occupying coniferous forest habitat (Adamonytė *et al.* 2012). After trees dry from the excrements and finally die, new nests are built, thereby spatially expanding the colony (Žydelis *et al.* 2002). The Juodkrantė cormorant colony is occupied from March, when the first birds return, and maximum nest occupancy occurs in April. Young

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appear at the beginning of May and stay in the nests till July. From mid-July, the cormorants disperse and in October they migrate southward.

The colony has great influence on forest stands, mainly due to guano increasing the nitrogen and phosphorus levels by 10^4 to 10^5 times, leading to the death of trees and formation of glades (Kameda *et al.* 2000, Laiviņš, Čekstere 2008, Garcia *et al.* 2011). Though soil fertility is increased, plant biomass is lower in the active colony (Kolb *et al.* 2010) and, after the birds disappear, shrub communities replace the dead forest (Żółkóś, Markowski 2006). It was shown that myxomycete diversity in the Juodkrantė colony was lower in the active part of the colony with the most fresh and numerous nests (Adamonytė *et al.* 2012).

So far, there have been no investigations on how the cormorant colony influences mammals. This paper intends to present the first data on the loss of diversity of the small mammal community in the area affected by the colony of great cormorants in Juodkrantė.

Material and Methods

Study area

The study area is located to the south of Juodkrantė settlement on the Curonian Spit, West Lithuania 55° 33' 10" N, 21° 07' 30" E) in the Curonian Spit National Park. Small mammal trapping was conducted in the various zones of the great cormorant colony (55° 31' N, 21° 06' E), as well as the margin between the inhabited zones and the surrounding forest and at a control site located in a nearby forest. According to duration and degree of the impact of great cormorants on the habitat, five zones were investigated (Fig. 1):

I – control zone. No influence of nesting cormorants on the habitat. Two habitat types dominating forests on the Curonian spit were investigated in the control zone – dry pine forest (Ia) and mixed forest (Ib). Trees in the control zone were somewhat younger than the dead trees within the colony. According Adamonytė et al. (2012), there are no remaining areas on the Curonian spit which fully correspond to the colony site in vegetation composition, age and position on the slope.

II – zone of initial influence of the colony. This part of the colony is currently expanding, thus is the most recent and the influence is just developing. Trees are still alive, but with reduced vitality, shrub layer reduced and herb layer is scarce. Moss layer is thin, with bare patches.

III – zone of long term influence of the colony. The highest concentration of nests is recorded in this zone. In the former oligotrophic pine forest, the trees are dead or dying and the shrub layer is reduced, formed by mesotrophic *Sorbus aucuparia* as well as by eutrophic *Sambucus nigra* and *S. racemosa* of low projection cover, and sparse, dying *Juniperus communis*. The projection cover of the herb layer is 10 % or less of predominantly nitrophilic species like ruderal *Chelidonium majus*; moss layer is absent (Adamonytė *et al.* 2012).

IV – zone of former active influence of the colony. Trees are dead, many of them rotten, fallen and decaying. The territory is re-growing with young trees and shrubs, the herbaceous layer is thick. Nitrophilic plant communities are establishing with sparse mesotrophic *Calamagrostis epigeios* that is supplemented by mesoeutrophic ruderal herbs and alien eutrophic *Sambucus nigra* and *S. racemosa*. Moss layer is absent (Adamonytė *et al.* 2012). Abandoned part of the colony with only few nests still in use.

V – zone of the ecotone between zones II and III and the surrounding forest that was not influenced by the colony.

Sampling

Small mammals were trapped with snap traps set in lines, each consisting of 25 traps spaced 5 m from each other. Traps were baited with bread and sunflower oil. They were left exposed for two or three days (one trapping session) and checked once a day (Balčiauskas 2004). In total, 51 snap trap lines were operated in September-October 2011 and May-November 2012, with total sampling effort of 3300 trap nights (Table 1). The relative abundance of small mammals was expressed as the number of individuals per 100 trap nights.

Small mammal communities in the different zones were characterized by their diversity (Shannon's H, on the base of log2 transformed data) and dominance (Simpson's c) (Krebs 1999, Balčiauskas 2004). Diversity indices were calculated from the pooled data.

Diversity assessment

Differences in small mammal diversity in different zones were tested using Rényi diversity numbers. Diversity profiles were calculated using scale parameter α between 0 and 4. Scale parameter α = 0 shows Rényi diversity equal to the logarithm of the number of species, α = 1 yields Rényi diversity equal to Shannon's H, α = 2 is related with Simpson's index of dominance, while α = 3 and 4 represent growing emphasis on the dominant species (Tóthmérész

Fig. 1. Trapping design in different zones of the great cormorant colony in Curonian Spit National Park in West Lithuania

1998). All diversity-related calculations (H±SD, c±SD and significance of difference) were performed in the freeware DOSBox ver. 0.74, running DivOrd program ver. 1.90 (Tóthmérész 1993). Differences in species composition of the communities were tested using chi-square test. All differences with $p > 0.05$ were considered non-significant. Differences in relative abundance were tested using non-parametric Kruskal Wallis H test for multiple groups and paired Kruskal Wallis ANOVA with Bonferroni correction. Calculations were done with Statistica for Windows, ver. 6.0 software (StatSoft 2004).

Results and Discussion

In 2011-2012, seven small mammal species were trapped in the different zones of the great cormorant colony and adjacent: common shrew (*Sorex araneus*), pygmy shrew (*S. minutus*), bank vole (*Clethrionomys glareolus*), meadow vole (*Microtus agrestis*), root vole (*M. oeconomus*), yellow-necked mouse (*Apodemus flavicollis*) and harvest mouse (*Micromys minutus*). The dominant species was *A. flavicollis*, accounting for 73.1% of all trapped individuals, with *C. glareolus* subdominant (22.2%). The proportion of other species was negligible (Table 2).

The diversity of small mammals was very low in all study plots (Table 2), as compared to other habitat types of the Curonian spit (Juškaitis, Ulevičius 2002). Five small mammal species were recorded both in the control zone and in the zone of former influence of the colony with abandoned nests. In the zones of initial and long term influence, the number of registered small mammal species was lower (3–4 species), whilst in the ecotone of these zones it is lowest (only two dominant species were found). The differences between the numbers of small mammal species between zones is also shown in Fig. 2A.

At $\alpha = 0$, Rényi diversity equal the logarithm of the number of species. At $\alpha = 1$ Rényi diversity numbers are equal to Shannon's H, while $\alpha > 1$ represents diversity of the higher order; $\alpha = 2$ represents dominance in the community (Tóthmérész 1998). From Fig 2A, it is clear that differences in diversity (Shannon's H) and dominance (Simpson's c) in small mammal assemblage are not well expressed between the five investigated zones of the great cormorant colony (values presented in Table 2). In the zone of initial influence of the colony, Shannon's H was significantly less than in the control zone ($t=1.96$, $p < 0.05$), in the zone of long term influence ($t=2.07$, $p < 0.05$) and in the zone of former influence of the colony ($t=2.53$, $p <$

0.01). Dominance was highest in the zone of initial influence of the colony. Compared with the zone of long term influence, zone of former influence and the ecotone zone, differences were significant at $p < 0.01$ (respectively, t=2.68. t=2.83 and t=2.78). Other differences were not statistically significant.

Comparing the least affected (I+IV) and the most affected (II+III+V) zones, we found that the diversity of the small mammal community was significantly higher in the less affected zone – Shannon's H respectively, was H = 1.17±0.005 and H = 0.98±0.005, while the difference in dominance was not significant – Simpson's c, respectively, was c = 0.58±0.004 and c = 0.60±0.004 (Fig. 2B).

The proportions of dominant *A. flavicollis* and subdominant *C. glareolus* in the small mammal community between the zones of the colony differed (see Table 2). A significantly higher proportion of *A. flavicollis* (90.3% of small mammals trapped, $\chi^2 = 5.19$, p = 0.02) and lower proportion of *C. glarelous* (6.5%, $\chi^2 = 4.92$, p = 0.03) was observed in zone II (the zone of initial influence of the expanding cormorant colony). In the zone V (the ecotone of zone II), the proportion of *A. flavicollis* was the lowest (67.4% of all trapped individuals, $\chi^2 = 0.99$, NS) and the proportion of *C. glareolus* the highest (32.7%, $\chi^2 = 3.63$, p = 0.06). No differences in the proportions of dominant and subdominant small mammal species in the community were observed when comparing the less affected (I+IV) and the most affected (II+III+V) zones

The average relative abundance of small mammals in the zones of the colony and surrounding areas was 12.00±1.50 ind. / 100 trap nights, with differences between the zones being statistically significant (Kruskal-Wallis test, $H_{4,51}$ =12.05 p =0.017). The highest relative abundance of small mammals was observed in zone V (ecotone). It was higher than in the zone of initial influence (Kruskal-Wallis ANOVA, $H_{1,13}$ =4.97 p =0.10) and in the control zone ($H_{1,21}$ =5.36 p =0.08). An abundance almost as high was also observed in the zone IV, former active influence of the colony. It was higher than in the zone of initial influence ($H_{1,20}$ =5.85 p =0.062) and in the control zone ($H_{1,28}$ =7.69 p =0.02).

In the control, no small mammals were trapped in a dry pine forest (Ia), while in a mixed forest (Ib) their relative abundance was 11.63±2.77 ind. / 100 trap nightss, i.e. higher than in the zones of initial (II) and long term (III) influence of the cormorant colony (Table 2, differences not significant).

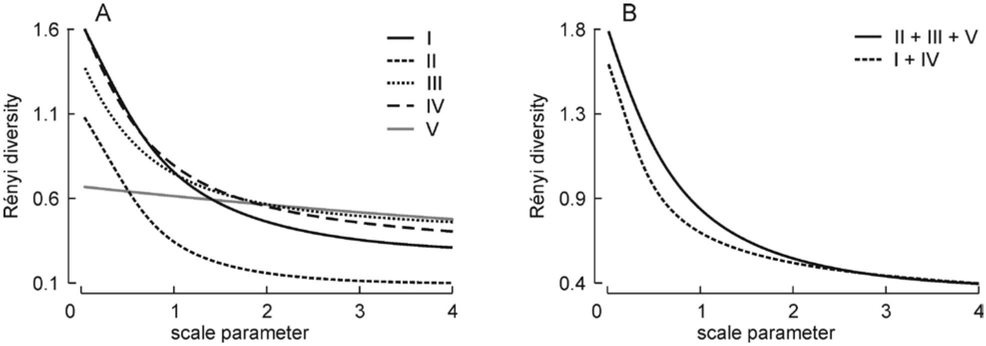

Fig. 2. Small mammal diversity in the zones of different influence of the great cormorant colony: A – differences between zones I-V, B – differences between the most affected (II+III+V) and the least affected (I+IV) zones, where I – control zone, II – zone of initial influence, III – zone of long term influence, IV – zone of former active influence and V – zone of the ecotone between zones II and III and the surrounding forest habitat. Scale parameter α = 0 gives Rényi diversity equal to the logarithm of the number of species, α = 1 yields Rényi diversity equal to Shannon's H, α = 2 is related with Simpson's index of dominance, while α = 3 and 4 represent growing emphasis on the dominant species (according Tóthmérész 1998)

Table 1. Trapping effort in different zones of the great cormorant colony, 2011–2012

	Zone				
	I	**II**	**III**	**IV**	**V**
Number of trap lines	16	8	10	12	5
Number of trap nights	1075	550	600	775	300
Area trapped, ha	28	3.2	4.2	4.6	1.6

Table 2. Number of trapped small mammals, their diversity (Shannon's H, Simpson's c) and relative abundance (RA, ind./100 trap nights) in the zones of different influence of the great cormorant colony (2011-2012), where I – control zone, II – zone of initial influence, III – zone of long term influence, IV – zone of former active influence and V – zone of the ecotone between zones II and III and the surrounding forest habitat. Subscripts show differences between groups, statistically significant at $p<0.05$ or higher level (t-test for Rényi diversity profiles, Kruskall Wallis ANOWA for relative abundance)

	Zones of the colony					**Total (n, %)**
	I	**II**	**III**	**IV**	**V**	
S. araneus	2	1	0	2	0	5 (1.6)
S. minutus	2	0	0	0	0	2 (0.6)
M. glareolus	10	2	15	29	16	72 (22.2)
M. agrestis	0	0	1	0	0	1 (0.3)
M. oeconomus	1	0	1	3	0	5 (1.6)
M. minutus	0	0	0	2	0	2 (0.6)
A. flavicollis	50	28	37	89	33	237 (73.1)
Total N	65	31	54	125	49	324 (100)
Number of species	5	3	4	5	2	7
Shannon's H±SD	1.11±0.02	$0.55\pm0.02^{I,III,IV}$	1.10±0.01	1.16±0.007	0.91±0.002	1.11±0.003
Simpson's c±SD	0.62±0.01	$0.82\pm0.01^{III,IV,V}$	0.55±0.01	0.56±0.006	0.56±0.009	0.59±0.002
RA±SE	8.00±2.34	7.50±2.06	10.40±4.01	18.67 ± 3.17^{I}	19.20±3.88	12.00±1.50

An earlier investigation of the small mammals on the Curonian Spit of Lithuania (Juškaitis, Ulevičius 2002) indicated that small mammal assemblages in the three types of forests in the Spit were extremely poor in species composition. Only three species (*S. araneus*, *A. flavicollis* and *C. glareolus*) were registered in coastal pine forests, while only two species occurred in black alder and birch stands. Average relative abundances were 8.8 ind. / 100 trap nights in the pine stands, 12.0 in the black alder and only 4.0 ind. / 100 trap nights in the birch stands. *A. flavicollis* and *C. glareolus* were co-dominants in the forests (Jujьkaitis, Ulevičius 2002). In the continental dry pine forests in South Lithuania, the relative abundance of *A. flavicollis* was 4-8 ind. / 100 trap nights, with that of *C. glareolus* being 0-8 ind. / 100 trap nights. The total number of species did not exceed four (Ulevičius, Juškaitis 2003). Thus, our results are in line with data of other research from pine forests in Lithuania.

The results of this research are valuable in several aspects. First of all, there are no published data on small mammal communities in landscapes influenced by large colonies of great cormorants. We discovered that in the most heavily influenced zones, the diversity and the relative abundance of the small mammal community decreased. The nitrogen and phosphorus loads in the Juodkrantė colony are extreme: in the soil of zones II, III and V, the quantity of nitrogen was 1.57-1.66 g per kg of soil, with phosphorus occurring at 0.29-0.39 g/kg. In zone IV, the area of former influence, the respective amounts were 2.87 and 0.93 g/kg.

At such high loads of the nutrients, small mammals can be influenced in various ways: for example, the ground is covered by faeces and fish remains in the breeding period of cormorants, noisy birds cause disturbance, acidity is higher than usual over the whole territory, the plant composition is altered, shelter is lacking in the zones of active influence, etc.

Small mammals cannot play role in nutrient cycling, when the load by birds is so high. Even in grassland ecosystems, small mammals bring in 3.5-4.0 kg/ha/year of nitrogen (Clark *et al.* 2005). While such an amount in natural ecosystems may alter nitrogen cycling, in the colony of great cormorants it is insignificant.

Nitrogen enrichment of the ecosystem, so heavily expressed in the great cormorant colony, does not only change plant communities, a phenomenon well-known and not requiring further proof (Odum, Barret 2005), but also results in changes in reproductive output and survival of juveniles; in the field ecosystem this may lead to a decrease in small mammal diversity (Parsons *et al* 2005). None of these possible effects were studied in the colony of great cormorants. In the future we are going to analyze reproduction parameters of the small mammals in different zones of the colony as well as their diet.

Conclusions

Our results showed that small mammal assemblage was different in the various zones of the colony of great cormorants. Primarily, reduction of species diversity was found in the most heavily bird-influenced parts of the colony. A significant impact was found in the zone of initial influence (expansion of the colony, short term impact) and in the zone of long term influence of the colony (colony established for a longer time, still active). The diversity of the small mammal community in these zones and their ecotone was lower than in the control zone and zone of former impact (most of the nests not used anymore). Only two species, dominant yellow-necked mouse *Apodemus flavicollis* and subdominant bank vole *Clethrionomys glareolus*, were numerous in all zones. The proportion of other five small mammal species, trapped in the territory of cormorant colony and in the control area nearby, was negligible. The relative abundance of small mammals was also lower in the territory of active zones than in the zone of former influence of the colony.

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References

Adamonytė G., Iršėnaitė R., Motiejūnaitė J., Taraškevičius R., D. Matulevičiūtė 2012. Myxomycetes in a forest affected by great cormorant colony: a case study in Western Lithuania. – *Fungal Diversity*, **13** (1): 131-146.

Balčiauskas L. 2004. Methods of investigation of terrestrial ecosystems. Part I. Animal surveys. Vilnius (VUL), 183 p.

Clark J. E., Hellgren E. C., Parsons J. L., Jorgensen E. E., Engle D. M., D. M. Leslie 2005. Nitrogen outputs from fecal and urine deposition of small mammals: implications for nitrogen cycling. – *Oecologia*, **144** (3): 447-455.

Garcia L.V., Ramo C., Aponte C., Moreno A., Dominguez M.T., Gomez-Aparicio L., Redondo R., T. Maranon 2011. Protected wading bird species threaten relict centenarian cork oaks in a Mediterranean biosphere reserve: a conservation management conflict. – *Biological Conservation*, **144** (2): 764-771.

Gražulevičius G., D. Elertas 2005. Didysis kormoranas Kuršių nerijoje [Great Cormorant in Curonian Lagoon]. – *Žurnalas apie gamtą*, **5** (11): 8-10.

Herrmann C., Bregnball T., Larison K., Ojaste I., K. Rattiste 2012. Population Development of Baltic Bird Species: Great Cormorant (*Phalacrocorax carbo sinensis*). HELCOM Baltic Sea Environment Fact Sheets for 2011. http://www.helcom.fi/BSAP_assessment/ifs/ifs2011/en_GB/cover/ (accessed 12.01.2013).

Ivanauskas T. 1938. Lietuvos paukščiai (Birds of Lithuania). T. 1., Kaunas (Jaunųjų ūkininkų ratelių sąjunga), 332 p.

Juškaitis R., A.Ulevičius 2002. Small mammals ot the Curonian Spit National Park. – *Theriologia Lituanica*, **2**: 34-46.

Kameda K., Koba K., Yoshimizu C., Fujiwara S., Hobara S., Koyama L., Tokuchi N., A Takayanagi 2000. Nutrient flux from aquatic to terrestrial ecosystem mediated by the Great Cormorant. – *Sylvia*, **36**: 54-55.

Kirikova T., Gregersen J., A. Grinchenko 2007. The development of the largest colony of the Great Cormorant (*Phalacrocorax carbo sinensis*) in Europe. – *Branta*, **10**: 175-182.

Kolb G. S., Jerling L., P. A. Hambäck 2010. The impact of cormorants on plant–arthropod food webs on their nesting islands. – *Ecosystems*, **13** (3): 353-366.

Krebs C. J. 1999. Ecological methodology. 2nd ed. Vancouver (Benjamin Cummings), 624 p.

Laiviņš M., G. Čekstere 2008 Kolonijās ligzdojošo zivju gārņu (*Ardea cinerea*) un jūraskraukļu (*Phalacrocorax carbo*) ietekme uz Latvijas ezera salu augu valsti un augsnēm. – *Mežzinatne*, **18** (51):74-84.

Ložys L., M. Dagys 2008. COST action 635 “INTERCAFE: Conserving Biodiversity – Cormorant-Fisheries Conflicts”. Interdisciplinary Initiative to Reduce pan-European Cormorant-Fisheries Conflicts”. Project report. Vilnius (Institute of Ecology of Vilnius University), 14 p.

Nemtzov S.C. 2008. Israel-Ukraine Cooperation for Experimental management of a Shared Overabundant population of Great Cormorants (*Phalacrocorax carbo*). Proceedings of 23rd Vertebrate Pest Conference. University of California, Davis, 108-112.

Odum E.P., G.W. Barret 2005. Fundamentals of ecology. 5th ed. CA (Thomson Brooks/Cole), 598 p.

Parsons, J.L., Hellgren, E.C., Jorgensen, E.E., D.M. Leslie 2005. Neonatal growth and survival of rodents in response to variation in maternal dietary nitrogen: life history strategy vs dietary niche. Oikos, 110(2): 297-308.

Pūtys Ž. 2012. Great cormorant *Phalacrocorax carbo sinensis* diet and its effect on fish community in the eutrophic Curonian Lagoon ecosystem. Summary of doctoral dissertation. Vilnius (VUL), 48 p.

Samusenko I.E. 2008. Dynamics and present status of the Cormorant (*Phalacrocorax carbo*) population in Belarus against a background of the development of problem “Cormorants – fish industry”. – *Branta*, **11**: 181-199.

Stanevičius V., S. Paltanavičius 1997. The Cormorant *Phalacrocorax carbo* in southern and eastern Lithuania. – *Ekologia* polska, **XLV** (1): 123-124.

StatSoft, Inc. 2004. STATISTICA (data analysis software system), version 6. www.statsoft.com

Tóthmérész B. 1998. On the characterization of scale-dependent diversity. – *Abstracta Botanica*, **22** (1-2): 149-156.

Tóthmérész B. 1993. DivOrd 1.50: a program for diversity ordering. – *Tiscia*, **27**: 33-44.

Ulevičius A., R. Juškaitis 2003. Mammals of the Dzūkija National Park (except bats). – *Theriologia Lituanica*, **3**: 11-29.

Žydelis R., Gražulevičius G., Zarankaitė J., Mečionis R., M. Mačiulis 2002. Expansion of the Cormorant (*Phalacrocorax carbo sinensis*) population in Western Lithuania. – *Acta Zoologica Lituanica*, **12** (3): 283-287.

Żółkóś K., R. Markowski 2006. Pressure of the Grey Heron breeding colony (*Ardea cinerea*) on the phytocoenosis of lowland acidophilous beech forest in the ‘Czapliniec w Wierzysku’ reserve (Kaszubskie Lake District). – *Biodiversity Research and Conservation*, **3-4**: 337-339.

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PAPER II

Mammals under a colony of great cormorants: population structure and body condition of yellow-necked mice

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Mammals under a colony of great cormorants: population structure and body condition of yellow-necked mice

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Abstract: Investigations into small mammals within the territory of a breeding colony of great cormorants (*Phalacrocorax carbo sinensis*), carried out in 2011–2014 near Juodkrantė (West Lithuania), demonstrated the colony's impact on the dominant rodent, yellow-necked mouse (*Apodemus flavicollis*). The age and sex structure of the sampled mice (n = 432), along with body weight, body condition index, and residuals from the linear regression, were used to analyse data from five zones of the colony and the surrounding forest. We found that in the most active zones of the cormorant colony, the age structure of the population was tilted towards a prevalence of juveniles, while sex structure was towards a prevalence of males ($P < 0.0001$). Despite males being significantly longer in body and heavier, body condition index was the same in both sexes. The effect of the zone of the colony was confirmed for body weight and its residuals; body length and body condition index (main effects ANOVA) were negative in the zones where cormorants were nesting actively.

Key words: *Phalacrocorax carbo sinensis*, breeding colony, *Apodemus flavicollis*, body condition

1. Introduction

Great cormorants (*Phalacrocorax carbo sinensis*) are able to form extremely large breeding colonies near water bodies; for example, there are 11,600 breeding pairs at Katy Rybackie in Poland, the largest tree-nesting colony in Europe (http://ec.europa.eu/environment/nature/cormorants/numbers-and-distribution.htm). In Lithuania, after 100 years of eradication, great cormorants started to breed again in 1989 (Stanevičius and Paltanavičius, 1997). The number of breeding pairs in the largest colony in the country, located near Juodkrantė, Kuršių Nerija (West Lithuania), was estimated at about 3000 in 2005–2010 (Pūtys, 2012), but was as high as 3800 breeding pairs in 2011 (Pūtys, 2012) and 3200 in the summer of 2012 (Dagys and Zarankaitė, 2013).

The influence of the colony on the environment is mainly due to an increase in N and P levels by 10^4 to 10^5 times, leading to death of the forest (Garcia et al., 2011). As the trees die, glades are formed and shrubs later replace the dead forest (Żółkóś and Markowski, 2006). Generally, in the active areas of the colony, plant biomass is decreased (Kolb et al., 2010).

The influence of the cormorant colony and an associated grey heron (*Ardea cinerea*) colony has already been shown on lichens (Żółkóś et al., 2013), fungi (Osono, 2012), plants (e.g., Anderson and Polis, 1999), insects, spiders, and lizards (Polis and Hurd, 1996). Due primarily to increased nitrogen levels, the abundance of herbivores and detritivores may increase.

In this colony of great cormorants in Lithuania, complex investigations into the influence of the colony on the ecosystem have been performed over the last few years as part of the National Research Programme "Ecosystems in Lithuania: Climate Change and Human Impact (2010–2014)". It has been shown that despite a general increase in the abundance of myxomycetes in the territory (Adamonytė et al., 2013), the most active part of the breeding colony alters fungal diversity in a negative way, with fungal abundance being at its lowest. The biggest decrease was observed in mycorrhizal species, but at the same time, coprophilous fungi appeared in the forest litter and specialised fungi species were recorded on plants (Kutorga et al., 2014). Due to altered pH, as well as the content of N, P, and Ca, lichen diversity was also affected, mostly in the active zone of the great cormorant colony (Motiejūnaitė et al., 2014).

So far, the only research into small mammals in colonies of great cormorants has been from Lithuania, showing a reduction in species diversity and a lower abundance in the most active parts of the breeding colony (Balčiauskienė et al., 2014).

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The aim of the current study was to determine if population structure and body condition of the dominant small mammal species, the yellow-necked mouse (*Apodemus flavicollis*), is affected by living in the zones of the great cormorant colony, with various intensities of influence by the breeding birds.

2. Materials and methods

We investigated the small mammal community living in the colony of great cormorants (*Phalacrocorax carbo sinensis*) and the surrounding territory, situated near Juodkrantė in Kuršių Nerija National Park (55°33′10″N, 21°07′30″E), West Lithuania. We defined five zones, each differing in the intensity and duration of the impact of the colony (Balčiauskienė et al., 2014).

The strongest and longest-lasting influence of the colony (Zone A, Figure 1) was recorded in the zone of long influence, which contained the greatest number of cormorant nests in 2011–2013. In Zone A, the shrub layer was scarce or significantly reduced, and trees were dying or dead (Figure 2A). Nitrophilic species of plants dominated in the herbage layer, the projection of which was less than 10% (Adamonytė et al., 2013).

Quite strong influence of the colony was observed in the expanding part of the colony, typified by fresh nests (Zone B, Figure 1). Shrub and herbage layers were scarce and trees were dying (Figure 2B). Bare patches without herbage or even moss were found on the ground.

The next zone was characterised by a strong former influence (Zone C, Figure 1) of the colony, but with most nests currently already abandoned by great cormorants. Dead and rotten trees were characteristic (Figure 2C). Tree saplings and shrubs were regrowing, the herbage layer was reestablishing, and the moss layer was absent (Adamonytė et al., 2013).

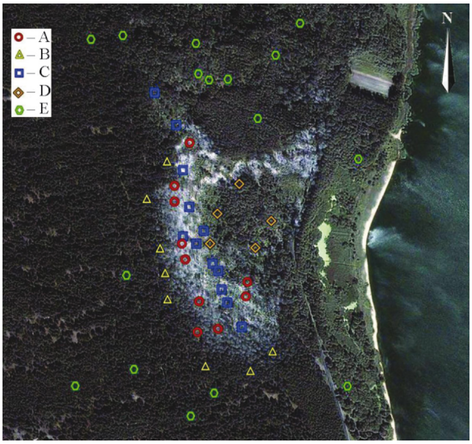

Figure 1. Location of Zones A–E in the colony of great cormorants near Juodkrantė, West Lithuania, 2011–2013.

Two other zones were characterised by even lower impact of the colony. We investigated Zone D (Figure 1, Figure 2D), which was the ecotone between the surrounding forest and Zones A, B, and C, and Zone E, which was a control zone, an area where the trapping of small mammals was performed at a distance from the colony. Two types of forest were characteristic of Zone E: dry pine forest and mixed forest.

The areas of the zones where small mammals were trapped were as follows: Zone A = 4.2 ha, Zone B = 3.2 ha, Zone C = 4.6 ha, Zone D = 1.6 ha, Zone E = 28 ha (Balčiauskienė et al., 2014).

Small mammals were trapped by snap traps, using lines of 25 traps each 5 m apart, baited with bread crust with sunflower oil, exposed for 3 days, and checked every day in the morning (Balčiauskas, 2004; Balčiauskienė et al., 2014). Trapping was done in September and October 2011; May, September, and November 2012; October and November 2013; and June 2014. Snap-trapping effort was equal to 4725 trap/days.

According to Lithuanian law, permission for small mammal snap-trapping is not required and thus was not issued by the Ministry of the Environment.

In addition, live trapping was performed in June, August, and September 2013; individuals found dead in live traps were added to the sample. Live-trapping effort was equal to 900 trap/days.

In total, 578 small mammal individuals (of 7 species) were trapped in the territory of the colony. The dominant species was yellow-necked mouse (*Apodemus flavicollis*): 432 individuals (74.7% of all catch) were trapped in the great cormorant colony and the control zone (Table 1).

Trapped small mammals were identified and weighed to an accuracy of 0.1 g. Standard measures were taken to an accuracy of 0.1 mm; the individuals were then dissected, with age and sex recorded. Three age categories were used, based on the presence and involution of the thymus gland and reproductive status of the animals (Prévot-Julliard et al., 1999). We examined the mammary glands, uteri, and ovaries in females; those with visible placental scars and corpora lutea, or who were pregnant or lactating, were defined as adults. Females with inactive reproductive organs, such as small nipples and closed vagina, were defined as subadults, while females with a thread-like vagina were classified as juveniles. Males with scrotal testes and full cauda epididymis were defined as adults, those with developed abdominal testes as subadults, and those with hardly visible testes as juveniles (Prévot-Julliard et al., 1999; Balčiauskas et al., 2012).

The age and sex structures of *A. flavicollis* in all zones were compared using chi-square statistics.

Figure 2. Zones A–D, in which small mammals were trapped in 2011–2014: Zone A – strongest and longest-lasting influence of the colony; Zone B – expanding part of the colony, Zone C – strong former influence; Zone D – ecotone zone between colony and surrounding forest.

Table 1. Sample size of *A. flavicollis* trapped in the colony of great cormorants near Juodkrantė, West Lithuania, 2011–2014.

Year	Males			Females			Both sexes together			
	Adult	Sub.	Juv.	Adult	Sub.	Juv.	Adult	Sub.	Juv.	Total*
2011	7	4	16	12	4	7	19	8	23	50
2012	32	33	23	16	27	39	48	71	63	187
2013	34	18	16	20	19	34	54	37	50	141
2014	23	2	9	19		3	39	2	12	54
Total	96	68	64	64	50	83	160	118	148	432

*: A few individuals, mainly destroyed by carnivores or insects, were not aged or sexed, and thus the total is bigger than the simple sum.

To define the body condition of the trapped individuals, we selected an index based on the ratio of body weight and body length (Drouhot et al., 2014). Such indices are used as indicators of animal health (Peig and Green, 2009). We used the body condition index $C = (Q/L^3) \times 10^5$, where Q is body weight in g and L is the body length in mm (Moors, 1985).

We applied GLM main effects ANOVA for body condition index C, body weight, and body length with year and month of trapping, zone, sex, and age of an individual as categorical predictors for testing of possible influence according to Tête et al. (2013).

Based on the assumption that body length is the best descriptor of body structure (Peig and Green, 2009; Tête et al., 2013), we regressed body weight against body length of every trapped individual, excluding pregnant females and individuals destroyed or eaten in traps by insects or carnivores from the sample. We used linear regressions and the least square method based on the high correlation between body weight and length. Due to the significant differences in body size, regressions for males and females were calculated separately. Structural body weight was obtained for every individual based on the regressions. Individuals with positive residuals were assumed to be in better condition as predicted by their size, and vice versa (Blackwell, 2002). We calculated the number of individuals in better and in worse condition for all five zones and tested their proportions using the chi-square test.

All calculations were done with Statistica 6.0 for Windows (www.statsoft.com).

3. Results

The sex and age structure of trapped *A. flavicollis* was different between zones of the great cormorant colony (Figure 3). The percentage of males significantly differed among the zones ($\chi^2 = 35.79$, df = 4, $P < 0.0001$), being highest in the zone of strongest and longest-lasting influence (over 70%). Females prevailed insignificantly only in the control zone.

The age structure of the trapped *A. flavicollis* was also different between zones of the colony: in the active zones, Zones A and B, the percentage of adult individuals was the lowest, while that of juvenile individuals the highest, at over 40%. In the control zone, Zone E, and in the ecotone between the colony and the surrounding forest, the percentage of adult mice was the highest at about 45%, while juveniles were less than 30% (Figure 3). Differences in the proportion of adult and subadult individuals ($\chi^2 = 32.02$) and the proportion of adult and juvenile individuals ($\chi^2 = 25.29$, both df = 4, $P < 0.0001$) between zones was significant, while the proportion of the subadult and juvenile mice was not ($\chi^2 = 3.38$, $P < 0.5$).

As for size, males of *A. flavicollis* were larger than females (body mass 38.02 ± 0.70 and 31.30 ± 0.60 g, respectively, Student's t = 7.09, df = 403, $P < 0.0001$). However, body condition was the same in both sexes, C = 3.31 ± 0.03 in males and C = 3.36 ± 0.05 in females, t = 0.94, P = 0.34. Following this, we regressed body weight against body length for males and females separately. In animals of both sexes, body weight was significantly correlated to body length (Figure 4).

Residuals of the standardised body weight of *A. flavicollis* showed that the influence of the great cormorant colony was negative (Table 2). Body condition in the control zone was balanced, i.e. there was a similar ratio of mice with greater and lower body weights than predicted by linear regression; for males it was 54% and 46% and for females it was 45% and 55%, i.e. 49% and 51% accordingly (differences not significant). In the zones influenced by the colony (A, B, and C), about 40% of mice had body weights greater than predicted, while 60% were smaller than predicted. This is significantly less than in Zone D, where the rate of *A. flavicollis* with body weights greater and smaller than predicted by linear regression was 65% and 35%, respectively (the difference significant for males, $\chi^2 = 10.95$, df = 1, $P < 0.001$; for females, $\chi^2 = 5.23$, $P = 0.02$; and for all individuals, $\chi^2 = 105.73$, $P < 0.0001$).

We found that the body weight of mice depended on trapping year and month, the zone, the sex of the animal, and age (main effects ANOVA, $F_{15,389} = 47.72$, $P < 0.0001$, $R^2 = 0.63$). All parameters analysed were highly significant for influence of the zone (Figure 5A). The body length of

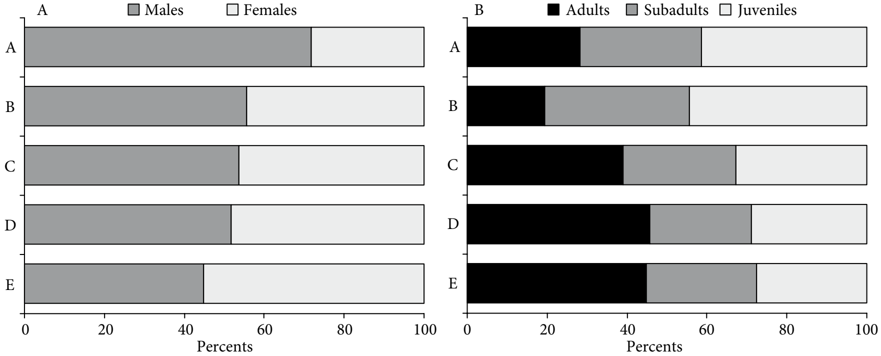

Figure 3. Sex (A) and age (B) structure of *A. flavicollis* trapped in 2011–2014 in the zones of the great cormorant colony (Zone A – strongest and longest-lasting influence of the colony; Zone B – expanding part of the colony; Zone C – strong former influence; Zone D – ecotone zone between colony and surrounding forest; Zone E – control).

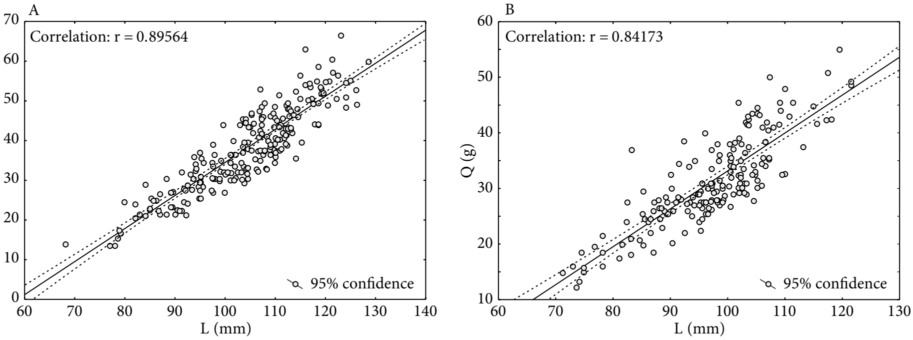

Figure 4. Correlation of the body weight and length of *A. flavicollis* trapped in 2011–2014 in the great cormorant colony: A – males, B – females.

Table 2. Distribution of residuals of standardised weight according to linear regression of *A. flavicollis* trapped in 2011–2014 in the zones of the great cormorant colony (Zone A – strongest and longest-lasting influence of the colony; Zone B – expanding part of the colony; Zone C – strong former influence; Zone D – ecotone zone between colony and surrounding forest; Zone E – control; positive residuals = body condition is better than predicted from body length, negative residuals = body condition is worse than predicted).

Zone	Males (n)		Females (n)		Total (n)	
	Positive	Negative	Positive	Negative	Positive	Negative
A	14	19	5	8	19	27
B	10	10	3	12	13	22
C	36	57	31	41	67	98
D	30	13	22	14	52	27
E	19	16	19	23	38	39

the mice was also influenced by all five parameters (main effects ANOVA, $F_{15,389} = 31.95$, $P < 0.0001$, $R^2 = 0.54$). The influence of the zone was also highly significant (Figure 5B). Variation of the body condition index was defined ($F_{15,387} = 6.53$, $P < 0.0001$, $R^2 = 0.17$) and was influenced mostly by the month of trapping ($F_{5,387} = 14.32$, $P < 0.0001$), and then by zone (Figure 5C) and year of trapping ($F_{3,387} = 2.71$, $P < 0.05$), but not by age or sex of the animal.

4. Discussion

In a colony of tree-nesting colonial birds, the main pressure on the environment is the input of nutrients, mainly nitrogen, phosphorus, and organic carbon (Breuning-Madsen et al., 2010). Depending on the N input from birds in nonproductive ecosystems, plants may be more productive (Anderson and Polis, 1999), resulting also in an increase in abundance of insects, spiders, and lizards (Polis and Hurd, 1996). Consumption of plants and detritus high in N may lead to an increase in the body size of herbivorous or detritivorous organisms (Anderson and Polis, 1999). However, negative impacts of the colonies are not uncommon in fungi (Osono, 2012; Adamonytė et al., 2013), lichens (Źółkóś et al., 2013; Motiejūnaitė et al., 2014), plants (Adamonytė et al., 2013), and insects (Kolb et al., 2012). Positive impacts may also be recorded in some species of lichens (Motiejūnaitė et al., 2014) and insects (Kolb et al., 2012).

Small mammal diversity in the active great cormorant colony is suppressed (Balčiauskienė et al., 2014). It is known that even small amendments of nitrogen negatively influence the survival of small mammals in a territory (Clark et al., 2005). However, not much is known about the underlying mechanism of the nitrogen impact; it has been shown that small granivores/omnivores might have higher N requirements than larger herbivores do (Parsons et al., 2005). It can only be said that landscape structure

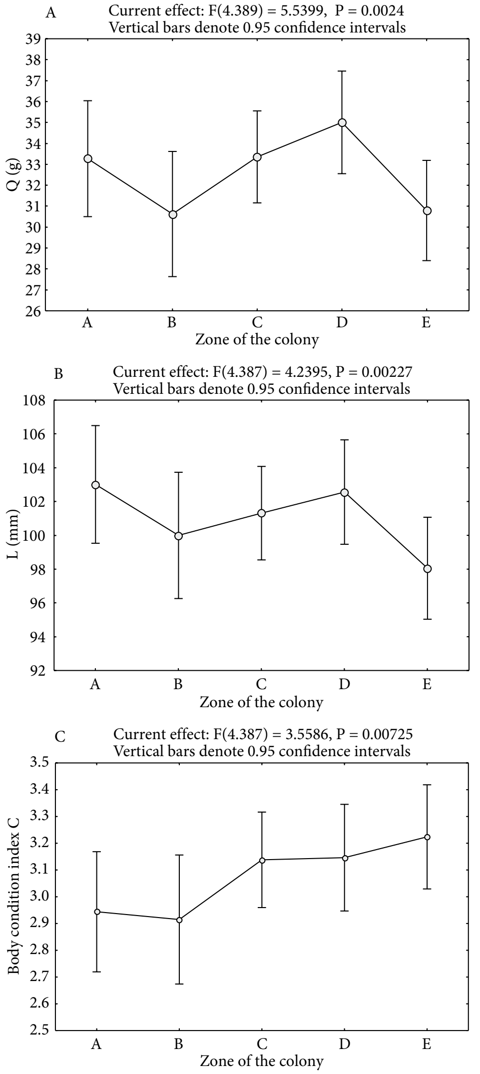

Figure 5. The influence of the zone on body weight (A), body length (B), and body condition index (C) of *A. flavicollis* trapped in 2011–2014 in the zones of the great cormorant colony (Zone A – strongest and longest-lasting influence of the colony; Zone B – expanding part of the colony; Zone C – strong former influence; Zone D – ecotone zone between colony and surrounding forest; Zone E – control).

influences long-term changes within small mammal communities (Schweiger et al., 2000), and thus, even after great cormorants stop breeding, the territory remains affected. In our study, this was the case in the zone of former strong influence (Zone C). Although the active influence of the colony in Zone C had already ceased, the amounts of N, P, and Ca in the soil of this zone in 2010–2011 were higher than in other zones of the colony, with a soil pH of 3.36 ± 0.28 (Adamonytė et al., 2013). In this zone, the diversity of myxomycetes had been somewhat restored (Adamonytė et al., 2013), and both nitrophilous lichens and those characteristic to mixed forests were recorded (Motiejūnaitė et al., 2014). As of yet, there have been no investigations on the time required for small mammals to reestablish diversity and abundance after cormorants no longer breed.

We found that the negative impact of the breeding colony of great cormorants in 2011–2014 was still present in the zone of former strong influence (Zone C). Body weight, body condition index, and population structure of the dominant small mammal, *A. flavicollis*, in this zone were similar to those of the zone of active colony influence, not to the control or ecotone zones. The same tendency was shown by the distribution of residuals of standardised weight against linear regression. In this respect, the influence of the colony is comparable to that of pollution shown in other species of the genus *Apodemus*, e.g., striped field mouse (*A. agrarius*) and wood mouse (*A. sylvaticus*) (Velickovic, 2007; Tête et al., 2013; Drouhot et al., 2014). However, due to short generation, intensive breeding, and migration, small mammals are able to rapidly recover as soon as the disturbance factor is removed (Bush et al., 2012).

The term "condition" or "body condition" may be used in quite different ways (Schulte-Hostedde et al., 2005). It is mainly used for the relation of the body weight to body size, where body length (Velickovic, 2007) or condylobasal skull length (Alcántara and Díaz, 1996) may be used as a size measure. A more sophisticated approach is to use residuals of standardised body weight or body condition index against linear regression, describing the relation of body size to mass (e.g., Schulte-Hostedde et al., 2005; Peig and Green, 2009, 2010). Linearity of relation between body size and weight is very important for the correct use of body condition indices (Schulte-Hostedde et al., 2005). For small mammals this relation is expected to be linear (Peig and Green, 2009, 2010), and so it was in our sample of *A. flavicollis*.

In small mammals, body weight and body condition may depend on many factors, among them animal sex, geographic location, habitat where the sample was collected, and pollution (Alcántara and Díaz, 1996; Díaz et al., 1999; Stevenson and Woods, 2006; Velickovic, 2007; Peig and Green, 2010; Tête et al., 2013; Drouhot et al., 2014). In turn, body weight and body condition may impact litter size (Evsikov et al., 2008). The complexity of factors determining body condition may explain why residuals from the linear regression explain only a small part of the variation in the body condition index in small mammals (Schulte-Hostedde et al., 2005).

Our results show that life in the territory under the nests of the breeding colony of great cormorants imposes consequences on the dominant small mammal, *A. flavicollis*. In the most intensively used territory, the population structure of *A. flavicollis* is biased towards a higher representation of males and young individuals. Generally, a biased sex ratio shows poor or disturbed habitat, or variation of the habitat quality over time (Julliard, 2000). In our case all three presumptions may work. In another study, males were prevalent in both mice and voles as an outcome of heavy grazing (Bush et al., 2012). It is quite possible that, in disturbed habitat, litters are male-biased due to higher cortisol level in mothers, as has been shown for ground squirrels (Ryan et al., 2012).

We also found that in the most intensively used zone, mice were characterised by smaller body weight and body condition indexes. Variation of the body weight and length was dependent on animal sex and age, but not the body condition index. Thus, differences in the age and sex structure of the mice trapped in different zones had no influence on results: despite a greater number of juvenile *A. flavicollis* and an insignificantly higher body condition index in this age group, the average body index was lower in the zone actively used by nesting cormorants. In conclusion, we confirm that the negative impact of the breeding colony of great cormorants was strongest in the most active zones of the colony.

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References

Adamonytė G, Iršėnaitė R, Motiejūnaitė J, Taraškevičius R, Matulevičiūtė D (2013). Myxomycetes in a forest affected by great cormorant colony: a case study in Western Lithuania. Fungal Divers 13: 131–146.

Alcántara M, Díaz M (1996). Patterns of body weight, body size, and body condition in the wood mouse *Apodemus sylvaticus* L.: effects of sex and habitat quality. In: Proceedings of the European Congress of Mammalogy I; 18–23 March 1991; Lisbon, Portugal. Lisbon, Portugal: Museu Bocage, pp. 141–149.

Anderson WB, Polis GA (1999). Nutrient fluxes from water to land: seabirds affect plant nutrient status on Gulf of California islands. Oecologia 118: 324–332.

Balčiauskas L (2004). Methods of Investigation of Terrestrial Ecosystems. Part I. Animal Surveys. Vilnius, Lithuania: VUL (in Lithuanian).

Balčiauskas L, Balčiauskienė L, Janonytė A (2012). Reproduction of the root vole (*Microtus oeconomus*) at the edge of its distribution range. Turk J Zool 36: 668–675.

Balčiauskienė L, Jasiulionis M, Balčiauskas L (2014). Loss of diversity in a small mammal community in a habitat influenced by a colony of great cormorants. Acta Zool Bulgar 66: 229–234.

Blackwell GL (2002). A potential multivariate index of condition for small mammals. New Zeal J Zool 29: 195–203.

Breuning-Madsen H, Ehlers-Koch C, Gregersen J, Løjtnant CL (2010). Influence of perennial colonies of piscivorous birds on soil nutrient contents in a temperate humid climate. Danish Journal of Geography 110: 25–35.

Bush ER, Buesching CD, Slade EM, Macdonald DW (2012). Woodland recovery after suppression of deer: cascade effects for small mammals, wood mice (*Apodemus sylvaticus*) and bank voles (*Myodes glareolus*). PLoS ONE 7: e31404.

Clark JE, Hellgren EC, Parsons JL, Jorgensen EE, Engle DM, Leslie DM (2005). Nitrogen outputs from fecal and urine deposition of small mammals: implications for nitrogen cycling. Oecologia 144: 447–455.

Dagys M, Zarankaitė J (2013). Status of the breeding population of Great Cormorants in Lithuania in 2012. In: Bregnballe T, Lynch J, Parz-Gollner R, Marion L, Volponi S, Paquet JY, Eerden MR, editors. National Reports from the 2012 Breeding Census of Great Cormorants *Phalacrocorax carbo* in Parts of the Western Palearctic. IUCN-Wetlands International Cormorant Research Group Report. Aahus, Denmark: Technical Report from DCE, Aarhus University, pp. 69–71.

Díaz M, Santos T, Tellería JL (1999). Effects of forest fragmentation on the winter body condition and population parameters of an habitat generalist, the wood mouse *Apodemus sylvaticus*: a test of hypotheses. Acta Oecol 20: 39–49.

Drouhot S, Raoul F, Crini N, Tougard C, Prudent AS, Druart C, Rieffel D, Lambert JC, Tête N, Giraudoux P et al. (2014). Responses of wild small mammals to arsenic pollution at a partially remediated mining site in Southern France. Sci Total Environ 470–471: 1012–1022.

Evsikov VI, Nazarova GG, Muzyka VY (2008). Body condition and reproductive characteristics of female water voles (*Arvicola terrestris* L.). Russ J Ecol 39: 414–417.

Garcia LV, Ramo C, Aponte C, Moreno A, Dominguez MT, Gomez-Aparicio L, Redondo R, Maranon T (2011). Protected wading bird species threaten relict centenarian cork oaks in a Mediterranean biosphere reserve: a conservation management conflict. Biol Conserv 144: 764–771.

Julliard R (2000). Sex-specific dispersal in spatially varying environments leads to habitat-dependent evolutionary stable offspring sex ratios. Behav Ecol 11: 421–428.

Kolb GS, Jerling L, Hambäck PA (2010). The impact of cormorants on plant–arthropod food webs on their nesting islands. Ecosystems 13: 353–366.

Kutorga E, Iršėnaitė R, Iznova T, Kasparavičius J, Markovskaja S, Motiejūnaitė J (2013). Species diversity and composition of fungal communities in a Scots pine forest affected by the great cormorant colony. Acta Mycol 48: 173–188.

Moors PJ (1985). Norway rats (*Rattus norvegicus*) on the Noises and Motukawao islands, Hauraki Gulf, New Zealand. New Zeal J Ecol 8: 37–54.

Motiejūnaitė J, Iršėnaitė R, Adamonytė G, Dagys M, Taraškevičius R, Matulevičiūtė D, Koreivienė J (2014). Pine forest lichens under eutrophication generated by a great cormorant colony. Lichenologist 46: 213–228.

Osono T (2012). Excess supply of nutrients, fungal community, and plant litter decomposition: a case study of avian-derived excreta deposition in conifer plantations. In: Young SS, Silvern SE, editors. Environmental Change and Sustainability. Rijeka, Croatia: InTech, pp. 173–196.

Parsons JL, Hellgren EC, Jorgensen EE, Leslie DM (2005). Neonatal growth and survival of rodents in response to variation in maternal dietary nitrogen: life history strategy vs dietary niche. Oikos 110: 297–308.

Peig J, Green AJ (2009). New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. Oikos 118: 1883–1891.

Peig J, Green AJ (2010). The paradigm of body condition: a critical reappraisal of current methods based on mass and length. Funct Ecol 24: 1323–1332.

Polis GA, Hurd SD (1996). Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. Am Nat 147: 396–423.

Prévot-Julliard AC, Henttonen H, Yoccoz NG, Stenseth NC (1999). Delayed maturation in female bank voles: optimal decision or social constraint? J Anim Ecol 6: 684–697.

Pūtys Ž (2012). Great Cormorant *Phalacrocorax carbo sinensis* Diet and its Effect on Fish Community in the Eutrophic Curonian Lagoon Ecosystem. Summary of PhD Dissertation. Vilnius, Lithuania: Institute of Ecology of Nature Research Centre, Vilnius University.

Ryan CP, Anderson WG, Gardiner LE, Hare JF (2012). Stress-induced sex ratios in ground squirrels: support for a mechanistic hypothesis. Behav Ecol 23:160–167.

Schulte-Hostedde AI, Zinner B, Millar JS, Hickling GJ (2005). Restitution of mass–size residuals: validating body condition indices. Ecology 86: 155–163.

Schweiger EW, Diffendorfer JE, Holt RD, Pierotti R, Gaines MS (2000). The interaction of habitat fragmentation, plant, and small mammal succession in an old field. Ecol Monogr 70: 383–400.

Stanevičius V, Paltanavičius S (1997). The Cormorant *Phalacrocorax carbo* in southern and eastern Lithuania. Ekologia Polska 45: 123–124.

Stevenson RD. Woods WA (2006). Condition indices for conservation: new uses for evolving tools. Integr Comp Biol 46: 1169–1190.

Tête N, Fritsch C, Afonso E, Coeurdassier M, Lambert JC, Giraudoux P, Scheifler R (2013). Can body condition and somatic indices be used to evaluate metal-induced stress in wild small mammals? PLoS ONE 8: e66399.

Velickovic M (2007). Measures of the developmental stability, body size and body condition in the black-striped mouse (*Apodemus agrarius*) as indicators of a disturbed environment in northern Serbia. Belg J Zool 137: 147–156.

Źółkóś K, Kukwa M, Afranowicz-Cieślak R (2013). Changes in the epiphytic lichen biota in the Scots pine (*Pinus sylvestris*) stands affected by a colony of grey heron (*Ardea cinerea*): a case study from northern Poland. Lichenologist 45: 815–823.

Źółkóś K, Markowski R (2006). Pressure of the Grey Heron breeding colony (*Ardea cinerea*) on the phytocoenosis of lowland acidophilous beech forest in the ‘Czapliniec w Wierzysku’ reserve (Kaszubskie Lake District). Biodiv Res Conserv 3–4: 337–339.

PAPER III

Skull variability of mice and voles inhabiting the territory of a great cormorant colony

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Skull variability of mice and voles inhabiting the territory of a great cormorant colony

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Abstract: We investigated the influence of a colony of great cormorants on the skull morphometry of yellow-necked mice (*Apodemus flavicollis*) and bank voles (*Myodes glareolus*) of three age groups trapped in the territory of the colony in 2011–2014. In general, most of the skull differences in both species were related to character length (skulls tended to become longer). In *A. flavicollis*, the skull size differences between zones were most expressed in subadult and adult individuals, while in *M. glareolus* they were most expressed in juveniles, with only a few characters different in adults and none in subadult voles. For both species, the largest skull characters were found mostly in the zone characterized by both the greatest number of cormorant nests and the longest and strongest influence by the colony. Concluding we confirm that the great cormorant colony has an influence on the skull morphometry of *A. flavicollis* and *M. glareolus* and we hypothesize that these differences enhance the ability of survival in specific conditions.

Key words: *Apodemus flavicollis*; *Myodes glareolus*; skull size; cormorant colony

Introduction

Great cormorants (*Phalacrocorax carbo sinensis* Staunton, 1796) are colonial nesting birds faithful to sites for many years. As such, they are able to alter the surrounding environment, mainly due to altered soil pH and the influx of nutrients into environment. Various influences on the ecosystem and their components have been shown (Klimaszyk & Joniak 2011; Osono 2012; Źółkóś et al. 2013; Klimaszyk et al. 2015).

Under the National Research Programme "Ecosystems in Lithuania: Climate Change and Human Impact (2010–2014)", the negative influence of a great cormorant colony was shown on the abundance of myxomycetes (Adamonytė et al. 2013), mycorrhizal and coprophilous fungi (Kutorga et al. 2013) and lichen diversity (Motiejūnaitė et al. 2014). The impact of a studied colony on small mammal species diversity and abundance is also negative (Balčiauskienė et al. 2014). The population structure of the dominant small mammal, namely yellow-necked mouse *Apodemus flavicollis* (Melchior, 1834), is biased towards a higher representation of males and young individuals in the territory used most intensively by great cormorants. Here, mice are characterised by smaller body weight and body condition indexes (Balčiauskas et al. 2015).

In the presented study, we tested if there are changes in skull morphometry in the two most dominant rodent species, *A. flavicollis* and bank vole *Myodes glareolus* (Schreber, 1780), inhabiting the territory of a great cormorant colony. We based our study on the presumptions that skull size differences may be found in small spatial (Schlanbusch et al. 2011) and temporal (Pergams & Lawler 2009) scales. Pollution and other environmental disturbances may have influence on the size of animal bones (Nunes 2001; Oleksyk et al. 2004; Velickovic 2007). Both rodent species are used for zoomonitoring purposes (Martiniaková 2010a).

The above-mentioned studies (Balčiauskienė et al. 2014; Balčiauskas et al. 2015) are the only studies devoted to small mammals inhabiting the territory of a colony of great cormorants. Our results illustrating differences in population structure and body condition warranted our current working hypothesis that skull size variability may also be driven by the influence of the colony.

Material and methods

Yellow necked mice (*A. flavicollis*) and bank voles (*M. glareolus*) were trapped between 2011–2014 in a colony of great cormorants (*P. carbo sinensis*) situated within the Kuršių Nerija National Park near Juodkrantė on the Curonian Spit in western Lithuania (55°33'10" N, 21°07'30" E). The Curionian Spit separates a shallow lagoon from the Baltic Sea and is 98 km long, narrow and comprised of sand dunes.

Here, related to the duration and intensity of the impact of the colony, five zones were defined (Adamonytė et al. 2013; Balčiauskienė et al. 2014; Balčiauskas et al. 2015):

1. Control zone (I): at a distance from the colony, dry pine forest and mixed forest;
2. Zone of initial influence (II): expanding part of the colony, characterised by scarce herb and shrub layers, dying trees and fresh nests;

Table 1. Craniometric data of *Apodemus flavicollis* from cormorant-affected and adjacent territory in Juodkrantė (all measurements in mm).

Skull character	Adults ($n = 111–179$)		Subadults ($n = 85–139$)		Juveniles ($n = 98–141$)	
	Avg ± SE	Min–max	Avg ± SE	Min–max	Avg ± SE	Min–max
X1	13.7 ± 0.05	12.0–15.0	13.2 ± 0.05	11.8–14.6	12.6 ± 0.05	11.0–13.9
X2	12.7 ± 0.06	10.6–14.2	12.3 ± 0.05	10.5–13.7	11.6 ± 0.06	9.9–13.2
X3	4.7 ± 0.02	3.9–5.3	4.4 ± 0.02	3.8–5.1	4.2 ± 0.02	3.5–5.0
X4	6.8 ± 0.03	5.6–7.8	6.5 ± 0.03	5.6–7.5	6.2 ± 0.04	5.2–7.4
X5	7.1 ± 0.03	5.8–8.5	6.8 ± 0.03	5.7–7.5	6.5 ± 0.04	5.4–7.8
X6	4.0 ± 0.02	3.3–7.1	3.8 ± 0.02	3.3–4.3	3.6 ± 0.02	3.1–4.2
X7	3.6 ± 0.01	3.2–4.0	3.6 ± 0.01	3.2–4.0	3.6 ± 0.01	3.1–4.0
X8	1.4 ± 0.00	1.2–1.6	1.4 ± 0.01	1.2–1.6	1.4 ± 0.01	1.2–1.6
X9	9.5 ± 0.05	6.8–10.8	9.1 ± 0.05	7.1–10.8	8.4 ± 0.06	6.7–10.1
X10	11.9 ± 0.03	11.0–13.8	11.8 ± 0.03	11.1–13.3	11.6 ± 0.03	10.8–12.4
X11	14.0 ± 0.06	11.5–15.7	13.4 ± 0.06	11.3–14.6	12.6 ± 0.07	10.8–14.4
X12	7.6 ± 0.04	6.1–10.0	7.3 ± 0.04	6.0–9.9	6.8 ± 0.04	5.4–7.9
X13	8.6 ± 0.04	7.4–9.8	8.4 ± 0.06	7.3–14.5	7.9 ± 0.04	6.8–8.8
X14	5.4 ± 0.02	4.0–6.1	5.2 ± 0.02	4.2–6.3	4.9 ± 0.03	4.0–5.8
X15	4.3 ± 0.01	4.0–4.6	4.3 ± 0.01	3.9–4.7	4.2 ± 0.01	3.8–4.7
X16	1.5 ± 0.01	1.3–1.9	1.5 ± 0.01	1.2–1.7	1.4 ± 0.01	1.2–1.7
X17	2.2 ± 0.01	1.3–2.6	2.1 ± 0.01	1.7–2.5	1.9 ± 0.01	1.5–2.4
X18	27.8 ± 0.16	23.0–31.3	27.6 ± 0.18	23.8–30.4	26.3 ± 0.19	22.1–29.2
X19	14.6 ± 0.05	12.1–16.0	14.2 ± 0.05	12.3–15.7	13.4 ± 0.07	11.4–14.9
X20	12.7 ± 0.05	10.8–13.8	12.2 ± 0.05	10.6–13.5	11.6 ± 0.06	10.4–13.1
X21	4.5 ± 0.02	3.9–5.2	4.4 ± 0.02	3.6–5.0	4.3 ± 0.02	3.4–5.0
X22	4.2 ± 0.01	3.7–4.6	4.2 ± 0.01	3.7–4.7	4.1 ± 0.01	3.8–4.6
X23	9.8 ± 0.05	8.6–11.0	9.7 ± 0.06	8.6–10.8	9.5 ± 0.06	7.9–10.9

3. Zone of the longest-lasting and strongest influence (III): held the greatest number of cormorant nests in 2011–2013. Nitrophilic species of herbs dominated in the herb layer, the projection of which is less than 10%. The shrub layer was scarce or significantly reduced, trees were dying or dead;

4. Zone of strong former influence of the colony (IV): most nests are already abandoned. Tree saplings and shrubs were re-growing, the herb layer re-establishing and the moss layer absent.

5. Zone of ecotone (V): between the surrounding forest and zones II–IV.

Small mammals were trapped with snap-traps, using standard 25-trap lines (2 lines per zone, traps 5 m apart each other, baited by bread crust with sunflower oil) and 3 days exposition (Balčiauskas 2004; Balčiauskienė et al. 2014). Trapping was conducted in September and October 2011, in May, September and November 2012, in October and November 2013, and in June and November 2014. Trapping effort was equal to 5335 trap/days.

Under dissection, animals were attributed to one of the three age categories, based on the presence and involution of the *gl. thymus* and reproductive status of the animals (Balčiauskas et al. 2012).

We analyzed the skulls of 468 *A. flavicollis* and 151 *M. glareolus*. Of these, for zones I, II, III, IV and V, the numbers of *A. flavicollis* individuals were 89, 38, 50, 185 and 106, and the numbers of *M. glareolus* individuals 18, 4, 17, 77 and 35, respectively.

The skulls were cleaned using *Dermestes* beetle larvae. Under a binocular microscope with a micrometric eyepiece which has an accuracy of 0.1 mm, 23 skull characters were measured. Only the characters of the right side of the skull were used. Measurements included: X1 – total length of mandibula at *processus articularis*, excluding incisors; X2 – length of mandibula excluding incisors; X3 – height of mandibula at, and including, first molar; X4 – maximum height of mandibula, excluding coronoid process; X5 – coronoid height of mandibula; X6 – length of mandibular diastema; X7 – length of mandibular tooth row; X8 – length of lower molar M1; X9 – length of *nasalia*; X10 – breadth of braincase, measured at the widest part; X11 – zygomatic skull width; X12 – length of cranial (upper) diastema; X13 – zygomatic arc length; X14 – length of *foramen incisivum*; X15 – length of maxillary toothrow; X16 – length of upper molar M1; X17 – incisor width across both upper incisors; X18 – condylobasal length; X19 – length of rostrum; X20 – length of the braincase; X21 – interorbital constriction; X22 – postorbital constriction; X23 – height of the braincase (according Balčiauskas & Balčiauskienė 2011).

We tested if differences in the size of skull characters were present and, if so, whether these differences were associated with possible drivers of change – i.e. zone of the colony, trapping year, trapping month, animal age and animal sex. Multifactor influence was tested using GLM (main effects ANOVA) for all skull measurements and all above-mentioned categorical predictors (according Tête et al. 2013). To evaluate differences in skull characters between zones, ANOVA was used. All calculations were done with Statistica for Windows, ver. 6.0 software (StatSoft 2004).

Results

The skull measurements of the different age groups of *A. flavicollis* are presented in Table 1. We found that sizes of these skull characters were significantly influenced by zone (Wilks $\lambda = 0.58$, $F = 1.33$, $P < 0.025$), year (Wilks $\lambda = 0.04$, $F = 18.32$, $P < 0.0001$) and month (Wilks $\lambda = 0.53$, $F = 1.25$, $P < 0.05$) of trapping, animal sex (Wilks $\lambda = 0.80$, $F = 2.30$, $P = 0.001$) and age (Wilks $\lambda = 0.47$, F = 4.18, $P = 0.0001$).

The aggregated influence of these five factors, including zone, was of different strengths. According mul-

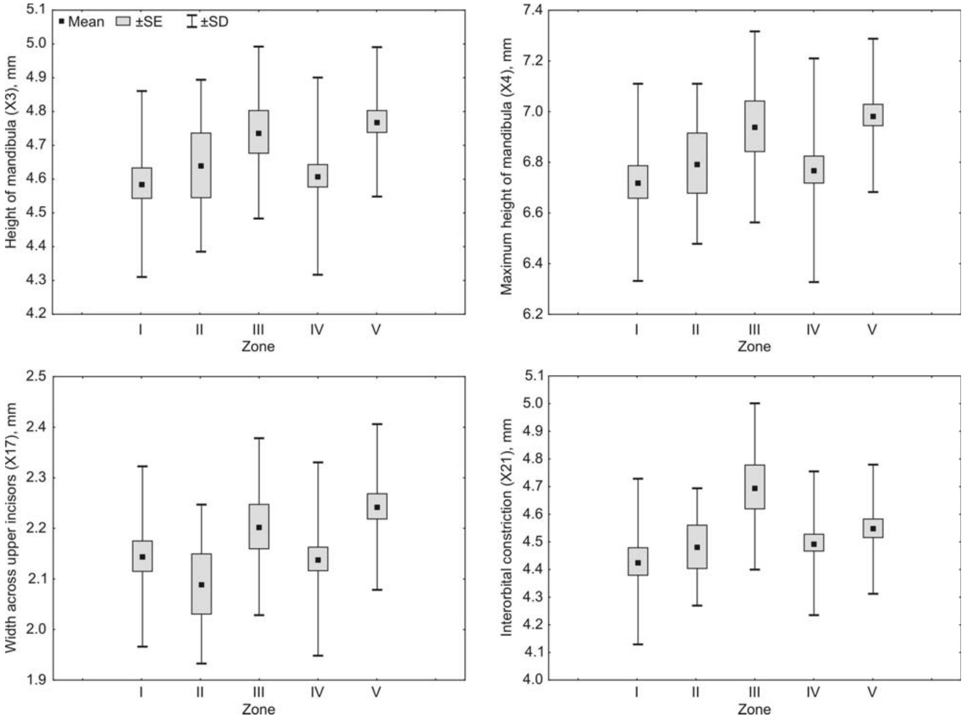

Fig. 1. Differences in skull characters of adult *Apodemus flavicollis* in the zones of the great cormorant colony. I – control zone, II – zone of initial influence, III – zone of the longest-lasting and strongest influence, IV – zone of strong former influence, V – zone of ecotone.

tiple determination coefficient, characters X7 and X15 were not influenced (i.e., were most stable) ($R^2 = 0.13$, $P < 0.005$), while X6, X8, X10, X16, X21 and X22 were weakly influenced ($R^2 = 0.15$–0.30, $P < 0.0001$), and X1–X5, X11–X14, X17 and X19–X20 were moderately influenced ($R^2 = 0.38$–0.48, $P < 0.0001$). X18 and X 23 were very strongly influenced (i.e. were most variable) ($R^2 > 0.70$, $P < 0.0001$).

The sizes of the skull characters of adult *A. flavicollis* in different zones of the cormorant colony are shown in Fig. 1. Although no significant differences were found in body measurements of animals (body mass highest in the zones II, III and V, smallest in zones I and IV, the same tendency with body length), differences in skull size between zones were significant for X3 (ANOVA, $F_{4,173} = 3.80$, $P < 0.006$), X4 ($F_{4,168} = 3.31$, $P = 0.012$), X17 ($F_{4,172} = 3.13$, $P = 0.016$) and X21 ($F_{4,166} = 3.03$, $P = 0.019$) and almost significant for X2 ($P = 0.06$), X5 ($P = 0.054$) and X20 ($P = 0.076$).

The influence of the zone on the skull size of subadult *A. flavicollis* was found to be stronger (Fig. 2). Significant size differences were found for X2 (ANOVA, $F_{4,133} = 3.30$, $P = 0.013$), X3 ($F_{4,134} = 2.88$, $P = 0.027$), X5 ($F_{4,126} = 2.78$, $P = 0.030$), X13 ($F_{4,121} = 4.02$, $P < 0.005$), X15 ($F_{4,131} = 2.58$, $P < 0.05$), X16 ($F_{4,132} = 2.53$, $P < 0.05$), X19 ($F_{4,129} = 2.66$, $P = 0.035$) and X21 ($F_{4,1262} = 3.59$, $P < 0.01$), while near significant for X14 ($F_{4,131} = 2.15$, $P = 0.078$) and X18 ($F_{4,84} = 2.64$, $P = 0.083$).

With juvenile *A. flavicollis*, there were no significant differences in skull measurements between zones (Fig. 3), but near-significant differences were recorded for X8 (ANOVA, $F_{4,136} = 2.39$, $P = 0.054$) and X21 ($F_{4,126} = 2.16$, $P = 0.078$).

The size of the skull characters of *M. glareolus* (Table 2) were most significantly influenced by the year of trapping (Wilks $\lambda = 0.007$, $F = 4.94$, $P < 0.0001$), then by animal age (Wilks $\lambda = 0.09$, $F = 2.72$, $P = 0.0002$) and sex (Wilks $\lambda = 0.26$, $F = 3.31$, $P = 0.002$) and month of trapping (Wilks $\lambda = 0.03$, $F = 1.66$, $P = 0.006$). Zone of the colony was not a significant influence (Wilks $\lambda = 0.07$, $F = 3.32$, $P = 0.37$).

Differences in the skull size of adult *M. glareolus* between zones, however, were significant for some characters (Fig. 4): X3 (ANOVA, $F_{4,34} = 2.88$, $P = 0.037$), X4 ($F_{4,34} = 3.25$, $P = 0.023$), X6 ($F_{4,34} = 3.38$, $P < 0.02$), X10 ($F_{4,24} = 3.37$, $P = 0.025$) and X20 ($F_{4,22} = 4.35$, $P = 0.009$), also near significant for X16 ($F_{4,35} = 2.45$, $P = 0.064$).

No significant differences in skull measurements for

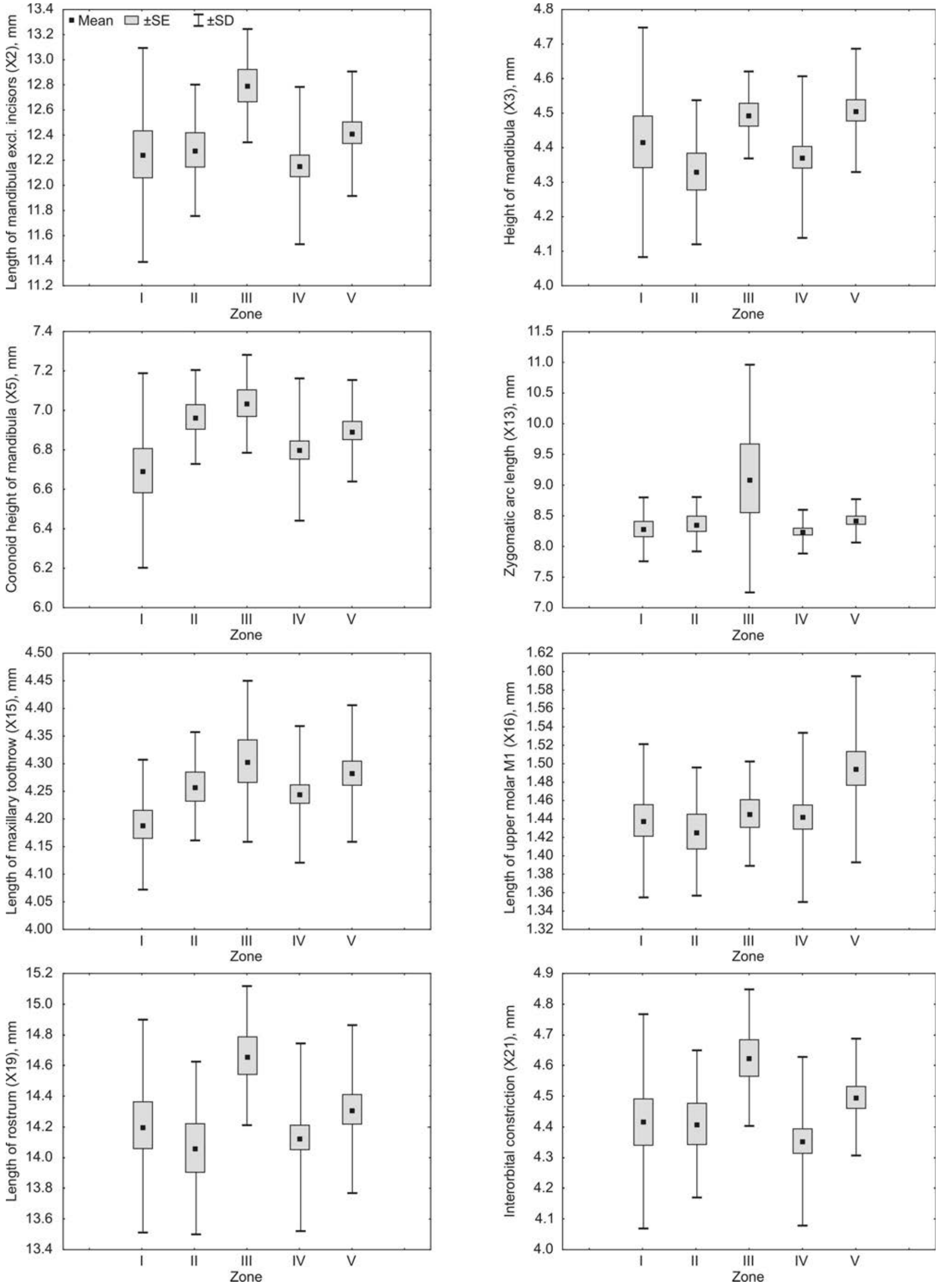

Fig. 2. Differences in skull characters of subadult *Apodemus flavicollis* in the zones of the great cormorant colony. I – control zone, II – zone of initial influence, III – zone of the longest-lasting and strongest influence, IV – zone of strong former influence, V – zone of ecotone.

Table 2. Craniometric data of *Myodes glareolus* from cormorant-affected and adjacent territory in Juodkrantė (all measurements in mm).

Skull character	Adults (n = 26–41)		Subadults (n = 27–40)		Juveniles (n = 40–66)	
	Avg ± SE	Min–max	Avg ± SE	Min–max	Avg ± SE	Min–max
X1	11.8 ± 0.07	10.9–12.9	11.5 ± 0.07	10.8–12.8	11.2 ± 0.04	10.4–12.0
X2	11.0 ± 0.05	10.3–11.8	10.8 ± 0.07	10.0–12.0	10.5 ± 0.05	9.5–11.3
X3	4.3 ± 0.03	4.0–4.6	4.2 ± 0.03	3.9–4.8	4.1 ± 0.02	3.6–4.5
X4	6.0 ± 0.04	5.4–6.6	5.9 ± 0.05	5.3–6.8	5.6 ± 0.03	4.9–6.2
X5	5.7 ± 0.03	5.4–6.2	5.7 ± 0.04	5.4–6.1	5.6 ± 0.04	4.6–6.1
X6	2.9 ± 0.02	2.6–3.2	2.9 ± 0.02	2.8–3.2	2.8 ± 0.02	2.5–3.3
X7	4.6 ± 0.02	4.2–5.0	4.6 ± 0.02	4.3–4.9	4.5 ± 0.02	3.7–4.8
X8	2.1 ± 0.01	1.9–2.3	2.1 ± 0.01	1.9–2.2	2.0 ± 0.01	1.6–2.4
X9	5.9 ± 0.06	5.0–6.8	5.6 ± 0.06	4.7–6.2	5.4 ± 0.05	4.2–6.4
X10	10.6 ± 0.04	10.2–11.0	10.6 ± 0.04	10.2–11.1	10.5 ± 0.03	10.1–10.9
X11	12.8 ± 0.06	12.1–13.6	12.4 ± 0.05	11.7–13.5	11.9 ± 0.05	10.8–12.7
X12	6.3 ± 0.04	5.9–7.1	6.0 ± 0.03	5.5–6.7	5.8 ± 0.03	5.1–6.3
X13	7.4 ± 0.05	6.8–8.0	7.2 ± 0.04	6.7–7.8	7.0 ± 0.04	6.2–7.5
X14	4.3 ± 0.03	3.9–4.7	4.1 ± 0.03	3.6–4.5	4.0 ± 0.03	3.3–4.9
X15	5.1 ± 0.02	4.9–5.6	5.1 ± 0.03	4.1–5.3	5.0 ± 0.02	4.2–5.3
X16	1.7 ± 0.01	1.6–1.8	1.7 ± 0.01	1.5–1.9	1.6 ± 0.01	1.5–1.8
X17	2.2 ± 0.02	2.0–2.6	2.1 ± 0.02	1.8–2.4	2.0 ± 0.02	1.6–2.3
X18	23.3 ± 0.20	21.3–24.6	22.1 ± 0.20	19.9–23.9	21.7 ± 0.15	20.1–23.3
X19	12.7 ± 0.07	11.9–13.4	12.3 ± 0.05	11.5–12.9	12.0 ± 0.05	10.5–12.7
X20	9.8 ± 0.06	9.3–10.4	9.4 ± 0.04	8.7–9.8	9.2 ± 0.05	8.4–9.8
X21	4.6 ± 0.04	4.0–5.2	4.6 ± 0.04	3.9–5.0	4.4 ± 0.02	4.0–4.9
X22	3.6 ± 0.02	3.3–3.9	3.6 ± 0.02	3.4–3.8	3.6 ± 0.01	3.3–3.8
X23	8.6 ± 0.08	7.8–9.3	8.4 ± 0.08	7.7–9.1	8.4 ± 0.08	7.7–9.3

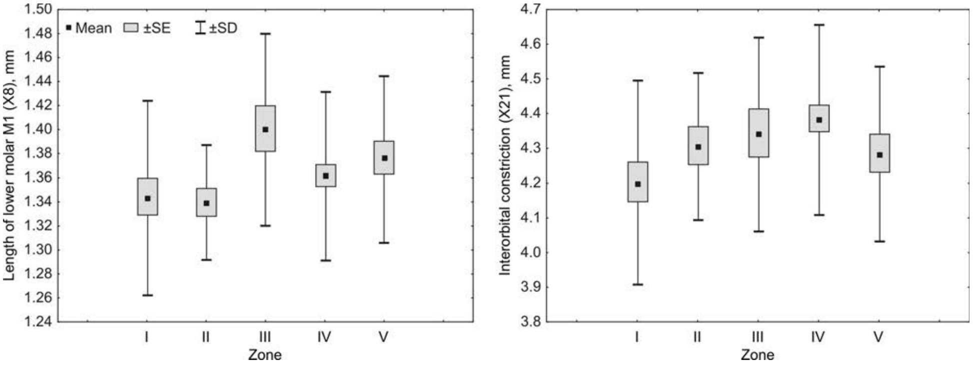

Fig. 3. Differences in skull characters of juvenile *Apodemus flavicollis* in the zones of the great cormorant colony. I – control zone, II – zone of initial influence, III – zone of the longest-lasting and strongest influence, IV – zone of strong former influence, V – zone of ecotone.

subadult *M. glareolus* between zones were found, and the only near-significant one was for X16 (ANOVA, $F_{3,35} = 2.80$, $P = 0.054$). However, no subadult individuals were trapped in the zone II and only one in zone III (the two zones most strongly influenced of the colony).

Contrary to the findings for *A. flavicollis*, the influence of the zone on the skull size of juvenile *M. glareolus* was present for many characters (Fig. 5). Significant differences were found for X6 (ANOVA, $F_{4,61} = 3.19$, $P < 0.02$), X14 ($F_{4,61} = 3.00$, $P = 0.025$), X18 ($F_{4,32} = 3.22$, $P = 0.025$), X21 ($F_{4,61} = 3.55$, $P = 0.011$) and X23 ($F_{4,32} = 3.32$, $P = 0.022$), while near-significant differences were found for X12 ($F_{4,61} = 2.43$, $P = 0.057$), X17 ($F_{4,60} = 2.28$, $P = 0.071$) and X19 ($F_{4,61} = 2.19$, $P = 0.080$).

Thus, in all age groups of *A. flavicollis*, the largest skull characters (10 cases, see Figs 1–3) were mostly found in zone III (i.e., the zone with the long-lasting and strongest influence, and with greatest number of cormorant nests), while in three cases (X17 for adult mice, X3 and X16 for subadult ones) the largest characters were found in zone V (ecotone).

In adult and juvenile *M. glareolus*, the largest skull characters (7 cases, see Figs 4 and 5) were also mostly registered in the zone III, while in two cases (X9 in adult voles and X6 in juveniles) they were in zone I

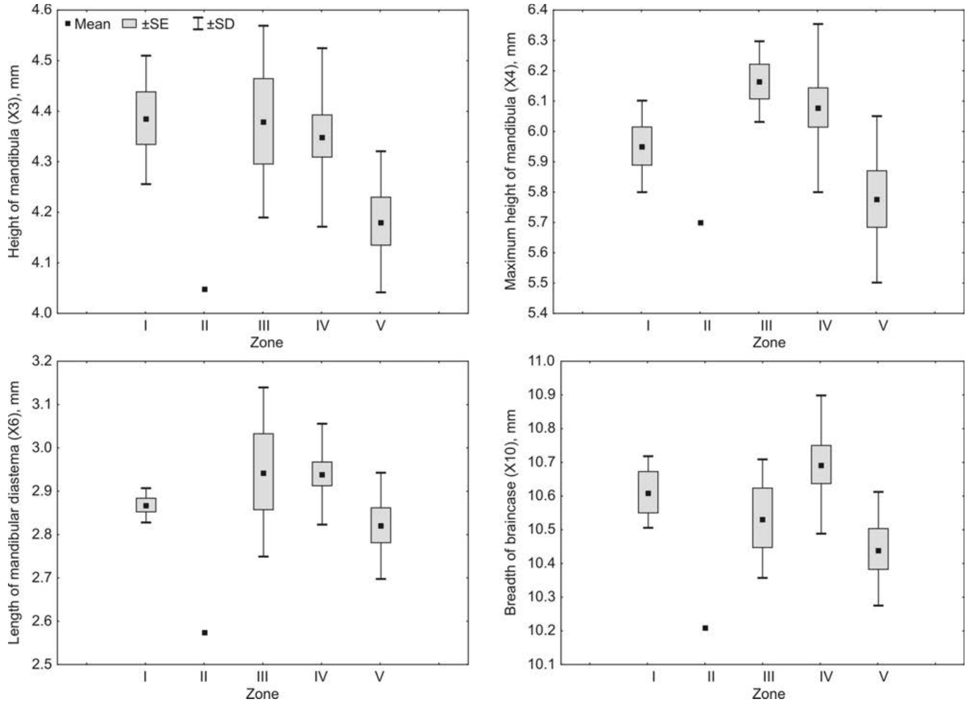

Fig. 4. Differences in skull characters of adult *Myodes glareolus* in the zones of the great cormorant colony. I – control zone, II – zone of initial influence, III – zone of the longest-lasting and strongest influence, IV – zone of strong former influence, V – zone of ecotone.

(control) and in one case (X2 in juvenile voles) in zone V.

Discussion

In the case of extreme disturbance, the response of small mammals may be nearly immediate. Populations under severe disturbance may exhibit greater-than-normal responses (Hendry et al. 1998). Life under the nests in the big colony of cormorants is by no doubts stressful to small mammals – in the oldest part of the colony, the forest ecosystem is destroyed and all coniferous trees are dead. Newly formed shrubs are mainly invasive black elderberry (*Sambucus nigra*) and red elderberry (*S. racemosa*), while greater celandine (*Chelidonium majus*) prevails in the herb layer and small balsam (*Impatiens parviflora*) is abundant. From the typical forest flora, only scarce hair grasses (*Deschampsia*) remain (Motiejūnaitė 2014).

Apodemus flavicollis and *M. glareolus* were chosen as the species for our study for several reasons. First of all, they are the dominant small mammal species living in the territory of the colony (Balčiauskienė et al. 2014) and only these two species are numerous enough to provide sufficient sample size. Secondly, both *A. flavicollis* and *M. glareolus* are well known as objects suitable for biomonitoring (Martiniaková 2010a; Petkovšek et al. 2014). These species may coexist (Grüm & Bujalska 2000) and they do not migrate (Martiniaková 2010b).

Within this very specific territory, i.e. the zones under varying influences of the colony of great cormorants, differences in the skull size of the two rodent species (*A. flavicollis* and *M. glareolus)* were observed in our study. In general, most of the skull differences of both species were related to character length. Skulls tended to become longer.

In *A. flavicollis*, the skull size differences between zones were most expressed in subadult and adult individuals, while in *M. glareolus* it was in juveniles, with only a few characters for adults and no differences found in subadult voles.

The largest skull characters of *M. glareolus* were recorded mostly in zone III (the long lasting and strongest influence by the colony), while for subadult *A. flavicollis* it was in zone III, and for adult *A. flavicollis* in both zone III and the ecotone zone between the zones of strongest influence of the colony and surrounding forest.

These differences accompany other differences already known at the level of the small mammal community (Balčiauskienė et al. 2014), population level and individual level (Balčiauskas et al. 2015). Among these, the most intensively used zones of the colony were associated with negative impacts such as reduced

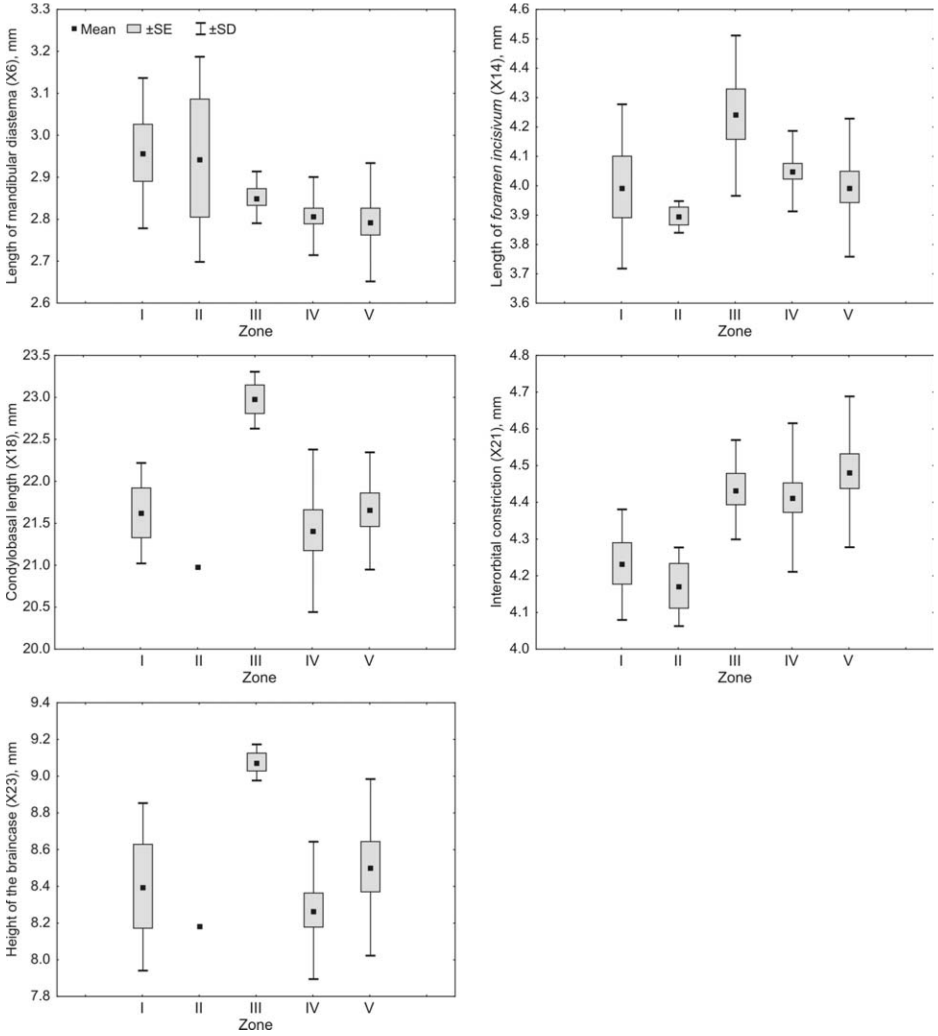

Fig. 5. Differences in skull characters of juvenile *Myodes glareolus* in the zones of the great cormorant colony. I – control zone, II – zone of initial influence, III – zone of the longest-lasting and strongest influence, IV – zone of strong former influence, V – zone of ecotone.

species diversity, changes in sex and age composition of the *A. flavicollis* population, a smaller body mass and poorer body condition.

It is known that in polluted areas animals are subjected to the influence of contaminants at spatial, temporal and media scales (Talmage & Walton 1991; Fritsch et al. 2011). Differences in the size of the animal or the size of skull morphometry may manifest themselves in very short spans (Schlanbusch et al. 2011). Host factors (sex, age, body size) also may influence observed differences (Veličković 2004; Fritsch et al. 2010; Rautio et al. 2010). For the body size of adults, it is important how long the individual had access to high quality food while growing (Yom-Tov et al. 2003). The trophic level (diet) (Jakimska et al. 2011) and feeding strategy (Johnson et al. 1996; Dayan & Simberloff 2005; van den Brink et al. 2010) could also be of high importance.

Food resources and differences in food availability in the various zones of the cormorant colony are among the expected drivers of the observed differences. The diet of *M. glareolus* is more variable between season and habitat, and more herbivorous than that of *A. flavicollis* (Bergstedt 1965; Heroldová 1994; Abt & Bock

1998). Thus it is possible that limited food resources in the territory of the cormorant colony are not sufficient to maintain high numbers of these voles. The diet of *A. flavicollis* is more stable across habitats (Abt & Bock 1998), more calorific and based on seeds and invertebrates (Gliwicz & Taylor 2002). In addition, *Apodemus* is a very environmentally tolerant species (Renaud et al. 2005). Thus, the dominance of *A. flavicollis* in all zones of the cormorant colony may be explained by the environmental tolerance of the species and its diet. However, the observed differences in skull size between zones may have other drivers.

By their influence on the environment, cormorant colonies may be considered as heavily polluted (Klimaszyk & Joniak 2011; Klimaszyk et al. 2015). As such, zones in the colony can be differentiated according to their influence and load of additional biogens (Adamonytė et al. 2013; Motiejūnaitė et al. 2014). Body and skull size differences may be driven by the gradient of pollution (Nunes 2001; Fritsch et al. 2010; Tête et al. 2013) and also reflect the disturbance of the habitat or the influence of the stress level (Oleksyk et al. 2004; Velickovic 2007; Hopton et al. 2009).

It is known that "environmental stress can increase phenotypic variation in populations by affecting developmental stability of individuals"; for example, vegetation removal influenced fluctuating asymmetry in shrews, and their mandible traits differed in sensitivity (Badyaev et al. 2000). Developmental instability was different in disturbed and undisturbed habitats (Hopton et al. 2009) and at different stress levels (Mooney et al. 1985). In our case, from early spring and through the breeding period, small mammals experience various stressors – among them, the presence and noise of cormorants, their constant droppings, the reduced amount of shelter due to forest and grass cover damage, reduced food choices and the presence of predators visiting the colony for other items of food (nestlings, fish remains, etc.; Jasiulionis unpubl.).

In conclusion, we confirm that the colony of great cormorant colony has an influence on the skull morphometrics of *A. flavicollis* and *M. glareolus* and hypothesize that these differences enhance the ability of survival in the local conditions. Furthermore, we suggest further investigations to discover whether these differences depend on the bioaccumulations or on peculiarities of feeding in the specific habitats in the colony.

Acknowledgements

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References

Abt. K. & Bock W.F. 1998. Seasonal variations of diet composition in farmland field mice *Apodemus* spp. and bank voles *Clethrionomys glareolus*. Acta Theriol. **43 (4):** 379–389. DOI: 10.4098/AT.arch.98-49

Adamonytė G., Iršėnaitė R., Motiejūnaitė J., Taraškevičius R. & Matulevičiūtė D. 2013. Myxomycetes in a forest affected by great cormorant colony: a case study in Western Lithuania. Fungal Diversity **59 (1):** 131–146. DOI: 10.1007/s13225-012-0203-8

Badyaev A.V., Foresman K.R. & Fernandes M.V. 2000. Stress and developmental stability: vegetation removal causes increased fluctuating asymmetry in shrews. Ecology **81 (2):** 336–345. DOI: 10.1890/0012-9658(2000)081[0336:SADSVR]2.0.CO;2

Balčiauskas L. 2004. Sausumos ekosistemų tyrimo metodai I dalis. Gyvūnų apskaitos [Methods of investigation of terrestrial ecosystems. Part I. Animal surveys]. VUL, Vilnius, 183 pp. ISBN: 9986196701

Balčiauskas L. & Balčiauskienė L. 2011. Estimation of Root Vole body mass using bone measurements from prey remains. North-West J. Zool. **7 (1):** 143–147.

Balčiauskas L., Balčiauskienė L. & Janonytė A. 2012. Reproduction of the root vole (*Microtus oeconomus*) at the edge of its distribution range. Turk. J. Zool. **36 (5):** 668–675. DOI: 10.3906/zoo-1111-20

Balčiauskas L., Balčiauskienė L. & Jasiulionis M. 2015. Mammals under a colony of great cormorants: population structure and body condition of yellow-necked mice. Turk. J. Zool. **39**: 941–948. DOI: 10.3906/zoo-1407-27

Balčiauskienė L., Jasiulionis M. & Balčiauskas L. 2014. Loss of diversity in a small mammal community in a habitat influenced by a colony of great cormorants. Acta Zool. Bulg. **66 (2):** 229–234.

Bergstedt B. 1965. Distribution, reproduction, growth and dynamics of the rodent species *Clethrionomys glareolus* (Schreber), *Apodemus flavicollis* (Melchior) and *Apodemus sylvaticus* (Liné) in southern Sweden. Oikos **16 (1/2):** 132–160. DOI: 10.2307/3564871

Dayan T. & Simberloff D. 2005. Ecological and community-wide character displacement: the next generation. Ecol. Lett. **8 (8):** 875–894. DOI: 10.1111/j.1461-0248.2005.00791.x

Fritsch C., Coeurdassier M., Giraudoux P., Raoul F., Douay F., Rieffel D., de Vaufleury A. & Scheifler R. 2011. Spatially explicit analysis of metal transfer to biota: Influence of soil contamination and landscape. PLoS ONE **6 (5):** e20682. DOI: 10.1371/journal.pone.0020682

Fritsch C., Cosson R.P., Cœurdassier M., Raoul F., Giraudoux P., Crini N., Vaufleury A. & Scheifler R. 2010. Responses of wild small mammals to a pollution gradient: Host factors influence metal and metallothionein levels. Envir. Pollut. **158 (3):** 827–840. DOI: 10.1016/j.envpol.2009.09.027

Gliwicz J. & Taylor J.R.E. 2002. Comparing life histories of shrews and rodents. Acta Theriol. **47 (Suppl. 1**): 185–208. DOI: 10.1007/BF03192487

Grüm L. & Bujalska G. 2000. Bank voles and yellow-necked mice: what are interrelations between them? Pol. J. Ecol. **48 (Suppl.):** 141–145.

Hendry A.P., Farrugia T.J. & Kinnison M.T. 2008. Human influences on rates of phenotypic change in wild animal populations. Mol. Ecol. **17 (1):** 20–29. DOI: 10.1111/j.1365-294X.2007.03428.x

Heroldová M. 1994. Diet of four rodent species from *Robinia pseudo-acacia* stands in South Moravia. Acta Theriol. **39 (3):** 333–337.

Hopton M.E., Cameron G.N., Cramer M.J., Polak M. & Uetz G.W. 2009. Live animal radiography to measure developmental instability in populations of small mammals after a natural disaster. Ecol. Indic. **9 (5):** 883–891. DOI: 10.1016/j.ecolind.2008.10.010

Jakimska A., Konieczka P., Skóra K. & Namiesnik J. 2011. Bioaccumulation of metals in tissues of marine animals, part II: metal concentrations in animal tissues. Pol. J. Environ. Stud. **20 (5):** 1127–1146.

Johnson M.S., Leah R.T., Connor L., Rae C. & Saunders S.1996. Polychlorinated biphenyls in small mammals from contaminated landfill sites. Envir. Pollut. 92 (2): 185–191. DOI: 10.1016/0269-7491(95)00096-8

Klimaszyk P. & Joniak T. 2011. Impact of black cormorant (*Phalacrocorax carbo sinensis* L.) on the transport of dissolved organic carbon from the catchment area to the lakes. Pol. J. Soil Sci. **42 (2):** 161–166.

Klimaszyk P., Brzeg A., Rzymski P. & Piotrowicz R. 2015. Black spots for aquatic and terrestrial ecosystems: impact of a perennial cormorant colony on the environment. Sci. Total Environ. **517:** 222–231. DOI: 10.1016/j.scitotenv.2015.02.067

Kutorga E., Iršėnaitė R., Iznova T., Kasparavičius J., Markovskaja S. & Motiejūnaitė J. 2013. Species diversity and composition of fungal communities in a Scots pine forest affected by the great cormorant colony. Acta Mycologica **48 (2):** 173–188. DOI: 10.5586/am.2013.019

Martiniaková M., Omelka R., Grosskopf B. & Jančová A. 2010a. Yellow-necked mice (*Apodemus flavicollis*) and bank voles (*Myodes glareolus*) as zoomonitors of environmental contamination at a polluted area in Slovakia. Acta Vet. Scand. **52:** 58. DOI: 10.1186/1751-0147-52-58

Martiniaková M., Omelka R., Jancová A., Stawarz R. & Formicki G. 2010b. Heavy metal content in the femora of yellow-necked mouse (*Apodemus flavicollis*) and wood mouse (*Apodemus sylvaticus*) from different types of polluted environment in Slovakia. Environ. Monit. Assess. **171 (1):** 651–660. DOI: 10.1007/s10661-010-1310-1

Mooney M.P., Siegel M.I. & Gest T.R. 1985. Prenatal stress and increased fluctuating asymmetry in the parietal bones of neonatal rats. Am. J. Phys. Anthropol. **68 (1):** 131–134. DOI: 10.1002/ajpa.1330680112

Motiejūnaitė J. 2014. Kormoranų poveikis gamtai [Impact of cormorants on nature]. Žurnalas „Miškai“ [Journal Forests] **10**: 24–26.

Motiejūnaitė J., Iršėnaitė R., Adamonytė G., Dagys M., Taraškevičius R., Matulevičiūtė D. & Koreivienė J. 2014. Pine forest lichens under eutrophication generated by a great cormorant colony. Lichenologist **46 (2):** 213–228. DOI: 10.1017/S002428 2913000820

Nunes A.C., Auffray J.C. & Mathias M.L. 2001. Developmental instability in a riparian population of the Algerian mouse (*Mus spretus*) associated with a heavy metal-polluted area in Central Portugal. Arch. Environ. Contam. Toxicol. **41 (4):** 515–521. DOI: 10.1007/s002440010279

Oleksyk T.K., Novak J.M., Purdue J.R., Gashchak S.P. & Smith M.H. 2004. High levels of fluctuating asymmetry in populations of *Apodemus flavicollis* from the most contaminated areas in Chornobyl. J. Environ. Radioact. **73 (1):** 1–20. DOI: 10.1016/j.jenvrad.2003.07.001

Osono T. 2012. Excess supply of nutrients, fungal community, and plant litter decomposition: a case study of avian-derived excreta deposition in conifer plantations, Chapter 10. pp. 173–196. DOI: 10.5772/26491 In: Young S.S. & Silvern S.E. (eds), Environmental Change / International Perspectives on Global Environmental Change, InTech, Rijeka, Croatia, 488 pp. ISBN: 978-953-307-815-1

Pergams O.R.W. & Lawler J.J. 2009. Recent and widespread tapid morphological change in rodents. PLoS ONE **4 (7):** e6452. DOI: 10.1371/journal.pone.0006452

Petkovšek S.A.S., Kopušar N. & Kryštufek B. 2014. Small mammals as biomonitors of metal pollution: a case study in Slovenia. Environ. Monit. Assess. **186 (7):** 4261–4274. DOI: 10.1007/s10661-014-3696-7

Rautio A., Kunnasranta M., Valtonen A., Ikonen M., Hyvärinen H., Holopainen I.J. & Kukkonen J.V.K. 2010. Sex, age, and tissue specific accumulation of eight metals, arsenic, and and selenium in the European hedgehog (*Erinaceus auropaeus*). Arch. Environ. Contam. Toxicol. **59 (4):** 642–651. DOI: 10.1007/s00244-010-9503-8

Renaud S., Michaux J., Schmidt D.N., Aguilar J.P., Mein P. & Auffray J.C. 2005. Morphological evolution, ecological diversification and climate change in rodents. Proc. R. Soc. B. Biol. Sci. **272 (1563):** 609–617. DOI: 10.1098/rspb.2004.2992

Schlanbusch P., Jensen T.S., Demontis D., Loeschcke V. & Pertoldi C. 2011. A craniometric investigation of the field vole *Microtus agrestis* in Denmark – population substructure. Hystrix **22 (2):** 227–255. DOI: 10.4404/Hystrix-22.2-4475

StatSoft, Inc. 2004. STATISTICA (data analysis software system), version 6. http://www.statsoft.com/textbook (accessed 15.01.2015).

Talmage S.S. & Walton B.T. 1991. Small mammals as monitors of environmental contaminants. Rev. Environ. Contam. Toxicol. **119:** 47–145. DOI: 10.1007/978-1-4612-3078-6_2

Tête N., Fritsch C., Afonso E., Coeurdassier M., Lambert J.C., Giraudoux P. & Scheifler R. 2013. Can body condition and somatic indices be used to evaluate metal-induced stress in wild small mammals? PLoS ONE **8 (6):** e66399. DOI: 10.1371/journal.pone.0066399

van den Brink N., Lammertsma D., Dimmers W., Boerwinkel M.C. & van der Hout A. 2010. Effects of soil properties on food web accumulation of heavy metals to the wood mouse (*Apodemus sylvaticus*). Environ. Pollut. **158 (1)**: 245–251. DOI: 10.1016/j.envpol.2009.07.013

Veličković M. 2004. Chromosomal aberrancy and the level of fluctuating asymmetry in black-striped mouse (*Apodemus agrarius*): effects of disturbed environment. Hereditas **140 (2):** 112–122. DOI: 10.1111/j.1601-5223.2004.01827.x

Velickovic M. 2007. Measures of the developmental stability, body size and body condition in the black-striped mouse (Apodemus agrarius) as indicators of a disturbed environment in northern Serbia. Belg. J. Zool. **137 (2):** 147–156.

Yom-Tov Y., Yom-Tov S. & Baagøe H. 2003. Increase of skull size in the red fox (*Vulpes vulpes*) and Eurasian badger (*Meles meles*) in Denmark during the twentieth century: an effect of improved diet? Evol. Ecol. Res. **5:** 1037–1048.

Żółkóś K., Kukwa M. & Afranowicz-Cieślak R. 2013. Changes in the epiphytic lichen biota in the Scots pine (*Pinus sylvestris*) stands affected by a colony of grey heron (*Ardea cinerea*): a case study from northern Poland. Lichenologist **45 (6)**: 815–823. DOI: 10.1017/S0024282913000558

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PAPER IV

The impact of Great Cormorants on biogenic pollution of land ecosystems: Stable isotope signatures in small mammals

Balčiauskas, L., Skipitytė, R., **Jasiulionis, M.**, Trakimas, G., Balčiauskienė, L., Remeikis, V.

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The impact of Great Cormorants on biogenic pollution of land ecosystems: Stable isotope signatures in small mammals

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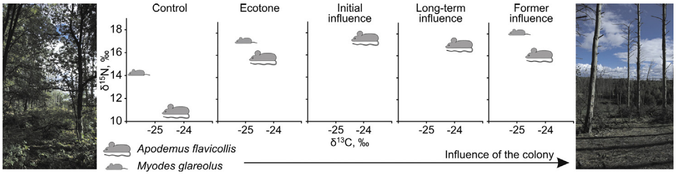
HIGHLIGHTS

- Cormorants transport nutrients from water to land ecosystems and pollute biogenically.
- We studied stable isotope composition of small mammal hair in 3 cormorant colonies.
- $\delta^{13}C$ and $\delta^{15}N$ were measured using elemental analyzer–isotope ratio mass spectrometer.
- $\delta^{13}C$ and $\delta^{15}N$ values were higher in rodents inhabiting cormorant colonies.
- Disruption of the ecosystem caused by Great Cormorant colonies affects small mammals.

GRAPHICAL ABSTRACT



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ABSTRACT

Studying the isotopic composition of the hair of two rodent species trapped in the territories of Great Cormorant colonies, we aimed to show that Great Cormorants transfer biogens from aquatic ecosystems to terrestrial ecosystems, and that these substances reach small mammals through the trophic cascade, thus influencing the nutrient balance in the terrestrial ecosystem. Analysis of $\delta^{13}C$ and $\delta^{15}N$ was performed on two dominant species of small mammals, *Apodemus flavicollis* and *Myodes glareolus*, inhabiting the territories of the colonies. For both species, the values of $\delta^{13}C$ and $\delta^{15}N$ were higher in the animals trapped in the territories of the colonies than those in control territories. In the hair of *A. flavicollis* and *M. glareolus*, the highest values of $\delta^{15}N$ (16.31 ± 3.01‰ and 17.86 ± 2.76‰, respectively) were determined in those animals trapped in the biggest Great Cormorant colony. $\delta^{15}N$ values were age dependent, highest in adult *A. flavicollis* and *M. glareolus* and lowest in juvenile animals. For $\delta^{13}C$ values, age-dependent differences were not registered. $\delta^{15}N$ values in both small mammal species from the biggest Great Cormorant colony show direct dependence on the intensity of influence. Biogenic pollution is at its strongest in the territories of the colonies with nests, significantly diminishing in the ecotones of the colonies and further in the control zones, where the influence of birds is negligible. Thus, Great Cormorant colonies alter ecosystem functioning by enrichment with biogens, with stable isotope values in small mammals significantly higher in the affected territories.

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1. Introduction

Small mammals (for example rodents) represent an important ecological group in terrestrial ecosystems (Bogdziewicz and Zwolak, 2014). They provide a base for trophic webs as they occur in great numbers and are usual prey for carnivores (Prevedello et al., 2013). The species composition of small mammals is not accidental: it depends on vegetation type and area, the food specialization of the small mammal species and various other influences. Small rodents channel nutrients and energy up to the higher trophic levels as they mostly utilize green plant material (*Microtus* spp), seeds and fruits and/or foods of animal origin (*Apodemus* spp., *Micromys* spp.) or feed on both low and high energetic plant resources and animal food (e.g. *Myodes glareolus*) (Renaud et al., 2005; Butet and Delettre, 2011; Čepelka et al., 2014). Information on changes in rodent communities and their food sources in natural and altered environments is key in the understanding of ecosystem functioning.

Colonies of Great Cormorants (*Phalacrocorax carbo*) are one of the factors that can most affect a terrestrial ecosystem. Cormorants deposit a lot of excreta at their nesting sites and play an important role in transporting nutrients from water to land ecosystems. They have a direct impact on forest ecosystem and damage vegetation through their breeding activities and excreta deposition (Ishida, 1996; Kameda et al., 2006; Klimaszyk et al., 2015). The impact is long-lasting as nutrient enrichment in the forest soil is significant not only in active colonies, but also in previously occupied areas abandoned by the birds (Hobara et al., 2001). Similarly, high nitrogen isotope ratios have been reported in the forest floor and living plants in areas both occupied by the cormorants and already abandoned (Kameda et al., 2006).

Despite recognizing cormorants as a vector of change in terrestrial ecosystems, their effects on autotrophs and consumers (e.g. rodent communities) are still poorly understood. Recent studies have shown that colonies of the cormorants significantly alter their environment by changing soil pH, nitrogen and phosphorus levels (Klimaszyk et al., 2015) and affecting lichens (Motiejūnaitė et al., 2014), fungi (Kutorga et al., 2013) and plants and arthropods (Kolb et al., 2010). Enrichment of the ecosystem by biogens and destruction of the typical woody vegetation imposes consequences on the small mammals in the territory, in particular a reduction in species diversity and decreased relative abundance of small mammals in the most heavily bird-influenced parts of the colony (Balčiauskienė et al., 2014). Within a cormorant colony, it was shown that the population structure of yellow-necked mice (*Apodemus flavicollis*) was biased toward a higher representation of males and young individuals in the most intensively used nesting area for the cormorants. Additionally, mice were characterized by smaller body weight and a lower average body index (Balčiauskas et al., 2015). Such a biased population structure is indicative of a poor or disturbed habitat or a variation of the habitat quality over time (Panzacchi et al., 2010; Sollmann et al., 2015). In the zones with both the highest number of cormorant nests and the longest-standing influence of the colony, *A. flavicollis* and bank voles (*Myodes glareolus*) also developed skull morphometric features that enhanced their ability to survive in specific conditions (Balčiauskienė et al., 2015).

Natural variability in the stable isotopic ratios of carbon, nitrogen and sulfur (δ^{13}C, δ^{15}N, δ^{34}S) is widely used in animal ecology, including studies of animal migration, food webs, trophic position estimation and food source reliance (Vander Zanden et al., 2015). Stable isotope analysis (SIA) has proven to be a useful tool in reconstructing diets, characterizing trophic relationships, elucidating patterns of resource allocation and constructing food webs, including diet (Boecklen et al., 2011).

Distributions of stable isotopes in investigated populations of animals can be a valuable technique for estimating trophic niche width (Bearhop et al., 2004) and finding differences in resource availability between sexes and age groups (Smiley et al., 2015). Stable isotope ratios can help to distinguish between resident animals and migrants (Hobson, 1999) as different environments have different stable isotope signals and this is reflected in the stable isotope ratios of the animal tissues. Using shaved hairs of the animals has the potential to be an effective non-lethal method for stable isotope measurements (Caut et al., 2008) and provides a direct technique to study feeding behavior in or between the populations. In small mammals, SIA has been used to investigate trophic segregation between two rodent species (Selva et al., 2012), dietary habits (Miller et al., 2008), trophic levels (Nakagawa et al., 2007) and trophic diversity and niche packing (Dammhahn et al., 2013).

A. flavicollis and *M. glareolus* are among the most common small mammals in European forest habitats. These species are good model organisms for examining nutrient and energy flow in forest ecosystems as they occur in high densities and have wide geographic ranges (Niedzialkowska et al., 2010). Using the SIA method, we studied the carbon and nitrogen isotope composition of *A. flavicollis* and *M. glareolus* hair in three Great Cormorant colonies and one cormorant-free forest in Lithuania. Stable carbon (δ^{13}C) and stable nitrogen (δ^{15}N) isotope ratios were measured. We aimed to show that Great Cormorants transfer biogens from aquatic ecosystems to land ecosystems, and that these substances reach small mammals through the trophic cascade, thus influencing the nutrient balance in the terrestrial ecosystem.

2. Material and methods

2.1. Study sites

Small mammals were trapped in 2014 in three Lithuanian colonies of *P. carbo*, situated in Juodkrantė (WGS 55° 31′ 14.22″, 21° 6′ 37.74″), Elektrėnai (54° 45′ 37.22″, 24° 40′ 41.45″) and Lukštas (55° 51′ 0.94″, 26° 12′ 6.11″). All three colonies had control zones. In addition, small mammals were also trapped at Zarasai (55° 44′ 46.36″, 25° 45′ 14.59″), a control site only with no breeding cormorants (Fig. 1).

The colony in Juodkrantė was formed in 1989 and is one of the largest in the Baltic Sea region: following a rise to 3303 pairs breeding in 2013, control measures reduced this to 1883 successful pairs in 2014 (with about the same number of unsuccessful nests). The area of the colony covers around 12 ha and several zones of differing levels of colony influence have been defined:

Zone I (the control zone with no direct influence by cormorants on the habitat).

Zone II (the zone of initial influence by the colony – the expanding part of the colony, thus only a recent and developing influence).

Zone III (the zone of long-term influence by the colony and with the highest concentration of nests).

Zone IV (the zone of former active influence by the colony with dead trees, many of them rotten, fallen and decaying).

Zone V (the zone of the ecotone between zones II and III and the surrounding forest).

These zones were described in detail by Balčiauskas et al. (2015). Additional information is given in Appendix (Fig. S1).

The two other studied colonies are much smaller and have never exceeded 200–300 breeding pairs. In 2014, 163 pairs successfully bred in Elektrėnai, while only 95 pairs in the Lukštas colony. The Elektrėnai cormorant colony is the oldest in Lithuania, forming in 1985 on a 6.5 ha island, 700 m from the nearest shore of the reservoir. The control zone for this colony was a cormorant-free part of the island, a distance >50 m from the nests. The Lukštas cormorant colony is the smallest and youngest colony in Lithuania. It is situated on a 1.3 ha peninsula in the northern part of Lukštas lake. The control zone of this colony was on the lakeshore, 200 m from the nests.

Control zones of the territories were selected on the basis of long-term knowledge of the Great Cormorant distribution and use of the surroundings of the colonies. To our knowledge, use of the control territories by these birds in Juodkrantė, Elektrėnai and Lukštas in 2014 was accidental and negligible. It is possible however that small amounts of biogens could have been transferred with seepage of rainwater.

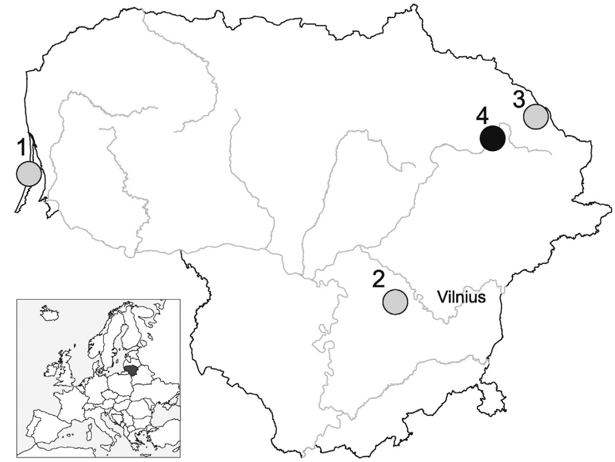

Fig. 1. Investigation sites in Lithuania. Great Cormorant colonies: 1 – Juodkrantė, 2 – Elektrėnai, 3 – Lukštas. Control site: 4 – Zarasai.

The control site Zarasai is situated 400 m from Žiegelis Lake with no cormorant colonies for a distance of at least 10 km. Small mammals were trapped in three habitats – natural meadow, young forest and pre-mature forest.

Additional information on the colonies is given in Appendix (Fig. S1–S4).

2.2. Small mammal sampling

Small mammals were trapped with snap traps set in lines, each consisting of 25 traps spaced 5 m from each other. Traps were baited with bread and sunflower oil. Exposition of traps was three days in Juodkrantė, Lukštas and Zarasai, one day in Elektrėnai. Total trapping effort for all colonies was equal 1600 trap days, control territories – 1000 trap days (Table 1).

In 2013, live trapping (three sessions, mid-June, end of August and end of September, 900 live trap nights) of the small mammals in the Juodkrantė colony for CMR (catch-mark-release) found that no movements of either *A. flavicollis* or *M. glareolus* occurred between the zones of the colony (unpubl. data).

2.3. Stable isotope analysis

Two species of small mammals, *A. flavicollis* and *M. glareolus* (dominants in the territory of the colonies) were used for SIA. Hair samples were taken from 117 individuals (41 *A. flavicollis* and 76 *M. glareolus*) by clipping off a tuft of hair between the shoulders of each specimen. Samples were placed in separate bags, labeled and stored dry for isotope analysis. Hair samples were scissored off, weighed with a microbalance and packed in tin capsules prior to the stable isotope analysis.

Table 1
Trapping effort (number of the trap/days) in the Great Cormorant colonies and control territories in 2014.

Site	Month	Colony	Control
Juodkrantė	September	600	150
Juodkrantė	November	600	150
Lukštas	September	300	300
Elektrėnai	October	100	100
Zarasai	November	–	300

Carbon and nitrogen stable isotope ratios were measured using an elemental analyzer (EA) (*Flash EA1112*) coupled to an isotope ratio mass spectrometer (IRMS) (*Thermo Delta V Advantage*) via a ConFlo III interface (EA-IRMS). A broader description of the equipment and its parameters is given by Garbaras et al. (2008).

Carbon and nitrogen isotope data are reported as δX values (where X represents the heavier isotope ^{13}C or ^{15}N) or differences from given standards, expressed in parts per thousand (‰) and are calculated according to the formula:

$$\delta X = \left[R_{sample}/R_{standard} - 1\right] \times 1000 \quad (1)$$

where $R_{sample} = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$ of the sample, $R_{standard} = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$ of the standard.

Reference materials Caffeine IAEA-600 ($\delta^{13}C = -27.771 \pm 0.043‰$, $\delta^{15}N = 1 \pm 0.2‰$) and oil NBS-22 IAEA ($\delta^{13}C = -30.031 \pm 0.043‰$) provided by the International Atomic Energy Agency (IAEA) were used as standards for calibration of the reference gases (CO_2 and N_2). EMA P2 (Elemental Microanalysis, $\delta^{13}C = -28 \pm 0.1‰$, $\delta^{15}N = -2 \pm 0.2‰$) was selected as a laboratory working standard. Repeated analysis of this reference material gave a standard deviation of <0.08‰ for carbon and 0.2‰ for nitrogen.

2.4. Statistical analysis

To describe the $\delta^{13}C$ and $\delta^{15}N$ values for all samples, the arithmetic mean ± 1 SE was used.

GLM Main effects ANOVA was used to test the influence of the species, site, territory (colony and control), animal gender and age on carbon and nitrogen stable isotope values, with Wilk's lambda to test the significance of influence. The post-hoc Tukey test was used for comparing multiple independent groups. Calculations were performed using Statistica (StatSoft. Inc., 2010). The minimum significance level was set at $p < 0.05$.

3. Results

Breakdown of results by Main effects ANOVA show, that distribution of stable isotopes was influenced by several factors – site, territory (colony or control), species, animal age and gender. Distribution of $\delta^{15}N$ was influenced most significantly ($r^2 = 0.77$, $F_{10,105} = 38.49$), that of $\delta^{13}C$ in similar extent ($r^2 = 0.64$, $F_{10,105} = 21.76$), both $p < 0.0001$). Distribution of N% was influenced in much lesser extent but still significantly ($r^2 = 0.18$, $F_{10,101} = 3.42$, $p < 0.001$), while distribution of C% did not depend on the mentioned factors ($F_{10,101} = 0.76$, NS). Univariate tests for significance revealed dependence of $\delta^{15}N$ from territory ($F_{3,105} = 13.30$, $p < 0.0001$) and species ($F_{1,105} = 9.79$, $p = 0.002$). Post hoc test showed, that species-related differences were significant for $\delta^{13}C$ (Tukey HSD, $p < 0.0001$), $\delta^{15}N$ ($p < 0.0002$), N% ($p < 0.0001$) but not C% ($p = 0.67$). In spite of these differences, further analysis was performed for two dominant species of small mammals, *A. flavicollis* and *M. glareolus*, separately (Table 2).

The atomic C/N ratios of all hair keratin samples measured in this study had a mean of 3.54 and standard deviation of 0.17, which is well within the range observed for hair samples, 3.00–3.80 (O'Connell and Hedges, 1999).

3.1. $\delta^{13}C$ and $\delta^{15}N$ values in *Apodemus flavicollis*

The distribution of $\delta^{13}C$ and $\delta^{15}N$ values in *A. flavicollis* individuals showed significant variation (Fig. 2). The distribution of $\delta^{15}N$ values were significantly different between colonies and control territories ($F_{2,33} = 7.30$, $p = 0.0012$) and in animal age groups ($F_{2,33} = 9.09$, $p = 0.0008$).

The highest $\delta^{15}N$ values were observed in the largest colony of Great Cormorants in Juodkrantė (Table 2), its average exceeding those in the Juodkrantė control territory (Tukey HSD, $p = 0.006$), Lukštas colony ($p = 0.0001$) and Lukštas and Zarasai control territories (both with $p = 0.0001$). The average value of $\delta^{15}N$ in *A. flavicollis* individuals registered in Juodkrantė control zone also exceeded the Lukštas colony ($p = 0.008$), Lukštas control ($p = 0.0002$) and Zarasai control territories ($p = 0.004$). *A. flavicollis* were not trapped in the Elektrėnai colony.

$\delta^{15}N$ values in adult *A. flavicollis* individuals (15.43 ± 0.83‰) were higher than those in subadults (12.84 ± 1.25‰, Tukey HSD, $p < 0.003$), and stable nitrogen isotope values in subadult animals were higher than those in juveniles (3.86 ± 0.50‰, $p < 0.0002$).

The distribution of $\delta^{13}C$ values in *A. flavicollis* showed no significant differences relating to animal age or gender. The average $\delta^{13}C$ value in *A. flavicollis* from the Lukštas colony was significantly lower than in the Juodkrantė colony of Great Cormorants (Tukey HSD, $p < 0.003$) and Juodkrantė control territory ($p < 0.05$).

The values of N% and C% in *A. flavicollis* did not differ between colonies and control territories (Table 2) or in respect to animal age or gender.

3.2. $\delta^{13}C$ and $\delta^{15}N$ values in *Myodes glareolus*

In *M. glareolus*, $\delta^{15}N$ values differed significantly between colonies and control territories ($F_{3,65} = 10.36$, $p < 0.0001$). The highest $\delta^{15}N$ values in the hair of *M. glareolus* were observed in the colony of Great Cormorants in Juodkrantė, exceeding those in the Lukštas colony (Tukey HSD, $p = 0.0001$), Elektrėnai colony ($p < 0.002$) and Lukštas, Elektrėnai and Zarasai control territories (all with $p = 0.0001$). $\delta^{15}N$ values in the hair of *M. glareolus* trapped in the Juodkrantė control territory was also very high (Table 2) and did not differ significantly from Juodkrantė colony (Tukey HSD, $p = 0.82$). The average $\delta^{15}N$ values in in the hair of *M. glareolus* from the Lukštas colony exceeded that in the Lukštas control territory (Tukey HSD, $p = 0.0002$), while the Elektrėnai colony was insignificantly higher than the Elektrėnai control territory ($p = 0.06$). $\delta^{15}N$ values in *M. glareolus* from the Zarasai control territory were significantly lower than from any other investigation site, control or colony (Tukey HSD, $p < 0.02$–0.0001). The average values of $\delta^{15}N$ in the hair of adult *M. glareolus* (11.72 ± 1.07‰) significantly exceeded those in young individuals (9.90 ± 0.90‰, Tukey HSD, $p < 0.05$).

$\delta^{13}C$ values in *M. glareolus* differed significantly between colonies and control territories ($F_{3,65} = 3.81$, $p = 0.014$). The highest $\delta^{13}C$ values were registered in the hair of the *M. glareolus* trapped in the cormorant colony in Juodkrantė (Table 2) and Juodkrantė control territory (Fig. 3), the former significantly higher than from all other sites (Tukey HSD, difference from the Elektrėnai colony $p < 0.05$, Elektrėnai control territory $p < 0.01$, other sites $p = 0.0001$). No differences in $\delta^{13}C$ values in *M. glareolus* hair from different age groups or between genders were observed.

No differences of N% from the hair of *M. glareolus* were observed between colonies and control territories, between different age groups or

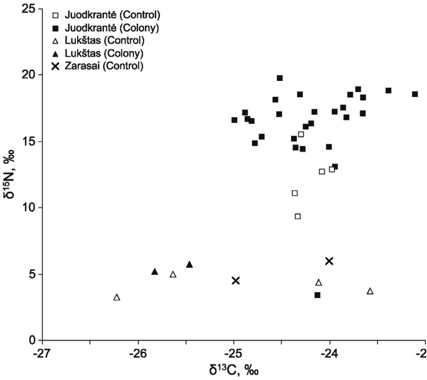

Fig. 2. Distribution of $\delta^{13}C$ and $\delta^{15}N$ values in *A. flavicollis* hair from the colonies of Great Cormorants and control territories.

Table 2
Central position (mean) and spread (standard error) of stable isotope ratios of *A. flavicollis* and *M. glareolus* in the colonies of Great Cormorants and control territories.

Site	Territory	n	$\delta^{13}C$, ‰	$\delta^{15}N$, ‰	C%	N%
Apodemus flavicollis						
Juodkrantė	Colony	28	−24.19 ± 0.48	16.31 ± 3.01	45.73 ± 1.93	15.81 ± 0.78
	Control	5	−24.20 ± 0.17	12.26 ± 2.32	45.09 ± 1.56	15.22 ± 0.2
Lukštas	Colony	2	−25.64 ± 0.27	5.46 ± 0.37	48.67 ± 1.72	16.78 ± 0.34
	Control	4	−24.89 ± 1.25	4.06 ± 0.71	47.81 ± 5.33	16.41 ± 1.57
Zarasai	Control	2	−24.47 ± 0.69	5.04 ± 0.95	43.79 ± 4.05	15.08 ± 1.68
Myodes glareolus						
Juodkrantė	Colony	16	−24.88 ± 0.97	17.86 ± 2.76	47.00 ± 2.93	15.27 ± 0.98
	Control	1	−25.82	14.30	35.90	13.21
Lukštas	Colony	22	−26.54 ± 0.80	10.46 ± 3.14	45.76 ± 3.15	14.60 ± 1.17
	Control	9	−27.48 ± 0.84	5.31 ± 1.00	45.29 ± 2.23	14.36 ± 0.57
Elektrėnai	Colony	6	−26.08 ± 0.67	12.62 ± 2.07	46.28 ± 2.91	14.87 ± 0.77
	Control	12	−26.02 ± 0.79	8.86 ± 2.91	46.76 ± 2.92	15.03 ± 0.99
Zarasai	Control	10	−26.74 ± 0.63	4.74 ± 1.03	45.80 ± 1.80	14.85 ± 0.31

gender groups. C% values from the hair of *M. glareolus* differed significantly between colony and control territories ($F_{3,64} = 4.74$, $p < 0.005$), with the lowest value registered in the Juodkrantė control territory (Tukey HSD, $p < 0.05–0.01$).

3.3. $\delta^{13}C$ and $\delta^{15}N$ values in small mammals depending on the influence of a Great Cormorant colony

A breakdown of the distribution of stable isotopes in *A. flavicollis* hair between different parts of the Great Cormorant colony from Juodkrantė (Fig. 4) with respect to animal gender and age revealed significant differences of $\delta^{15}N$ values (main effects ANOVA, zone of the colony, Wilks lambda = 0.17, $p < 0.002$; age, Wilks lambda = 0.16, $p < 0.0001$). The lowest $\delta^{15}N$ values (average 10.98 ± 0.99‰) were registered in the hair of individuals trapped in the control zone of the Great Cormorant colony in Juodkrantė (Fig. 4). In the zones of the colony influenced by cormorants, $\delta^{15}N$ values in the hair of *A. flavicollis* were higher than in the control zone: zone II (average $\delta^{15}N = 17.58 \pm 0.93$‰, Tukey HSD, $p < 0.003$), zone III (average $\delta^{15}N = 17.05 \pm 0.73$‰, $p = 0.001$), zone IV (average $\delta^{15}N = 16.14 \pm 1.37$‰, $p = 0.001$) and zone V (average $\delta^{15}N = 15.89 \pm 0.49$‰, $p = 0.002$). Significant differences in $\delta^{13}C$, C% and N% in the hair of *A. flavicollis* trapped in different zones of the Great Cormorant colony from Juodkrantė were not found.

Young *A. flavicollis* from Juodkrantė were characterized by lower $\delta^{15}N$ values in their hair than those of adult and subadult individuals (Tukey HSD, both $p < 0.0002$).

In the Juodkrantė colony, *M. glareolus* were not trapped in the zones with ongoing fresh influence by Great Cormorants. The lowest $\delta^{15}N$ values were registered in the hair of individuals trapped in the control zone (zone I, average 14.30 ± 3.02‰), then higher in the ecotone (17.41 ± 1.59‰) and highest in zone IV (18.22 ± 0.92‰). These differences however were not significant. No differences were found regarding animal age.

4. Discussion

The measurements of stable isotopes in various animal tissues reflect the diets of these animals (Smith et al., 2009; Codron et al., 2012) and the metabolic rate of the tissue (Tieszen et al., 1983). SIA eliminates the shortcomings of traditional dietary investigations and are based on carbon and nitrogen isotopes (Dalerum and Angerbjörn, 2005) and hair samples of small mammals contain information on their diet for several months. However, this isotope method may fail to separate granivores from insectivores (Van den Heuvel and Midgley, 2014). Despite the possible limitations though, SIA has been widely used in small mammals to analyze trophic interactions and/or food competition (Robb et al., 2012; Bauduin et al., 2013), aspects of trophic niche differentiation and microhabitat segregation (Dammhahn et al., 2013), effects of habitat change (Bergstrom, 2013), human influence on habitats, such as forest logging (Nakagawa et al., 2007), and reconstruction of the former palaeoenvironmental and palaeoclimatic conditions (Gehler et al., 2012).

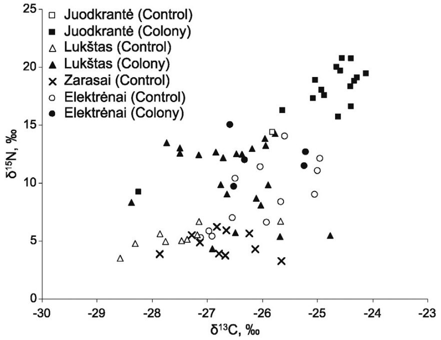

Fig. 3. Distribution $\delta^{13}C$ and $\delta^{15}N$ values in *M. glareolus* hair from the colonies of Great Cormorants and control territories.

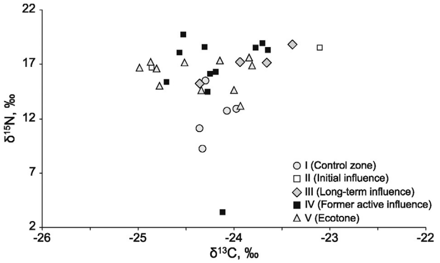

Fig. 4. Distribution $\delta^{13}C$ and $\delta^{15}N$ values in the hair of *A. flavicollis* trapped in the zones of Juodkrantė colony with different influence by Great Cormorants.

We used SIA on small mammals inhabiting the territories of the cormorant colonies as a tool to understand how nutrients, transported by Great Cormorants from the aquatic ecosystems (sea and lakes) to the terrestrial ecosystems, are changing the nutrient balance and to see if they reach small mammals through the trophic cascade. Freshwater and marine feeding can differ in several permils and reservoir effects occur. Stable isotope ratios in animal tissues reflect the source of the material and can vary depending on the system from which they derive. When biogens with their isotope signals are passed by birds from one system to the other, they are distributed in the new system and are carried to the next trophic levels. It has been shown that SIA may reflect resource partitioning of nutrient flows in food chains (Crawford et al., 2008). From previous studies, we know that small mammal populations and communities deteriorate in various ways under the influence of Great Cormorants, including reduced abundance, a reduction in species diversity, a biasing of the age and sex structures in populations, a lowering of body weight and a lower body condition index (Balčiauskienė et al., 2014; Balčiauskas et al., 2015; Balčiauskienė et al., 2015).

Results of the current research unambiguously show that the values of $\delta^{13}C$ and $\delta^{15}N$ in small mammals trapped in the territory of Great Cormorant colonies were extremely high (see Table 2). These values were significantly higher than those in the individuals of the same species trapped in control areas. Moreover, the $\delta^{15}N$ values in *A. flavicollis* were dependent on the intensity and time of existence of the colony (Fig. 4). The $\delta^{13}C$ and $\delta^{15}N$ values in the small mammals inhabiting territories of Great Cormorant colonies are higher than the values in the cormorants and have higher average values than other herbivores and carnivores (Table 3). Over-estimating the reliability of data collected from literature may be a problem in interpreting plausible differences (Boecklen et al., 2011), however in our case the differences are significant.

How can we interpret such unusual data? Several mechanisms may work simultaneously. The high nitrogen stable isotope ratios observed in small mammals in the Juodkrantė cormorant colony could be explained by the “fertilization effect” on the environment. Szpak et al. (2012) showed that plants fertilized by seabird guano were greatly enriched in $\delta^{15}N$ in comparison to control plant (by 11.3 to 20‰), as organic fertilizers have the capacity to alter the nitrogen isotopic composition of plants. Also, high nitrogen stable isotopic ratios in cormorant colonies have been observed in other studies. For example, Kameda et al. (2006) reported unusually high nitrogen stable isotopic ratios, e.g.

Table 3
Distribution of mean δ^{13}C and δ^{15}N values in various organisms, showing the position of small mammals trapped in Great Cormorant colonies and their control territories. Data sources for other mammals – Urton and Hobson (2005); Dekker and Hofmeester (2014); for Great Cormorants from the Juodkrantė colony – Morkūnė (2011); for fish, molluscs and insects – Rakauskas (2014).

Organisms	Mean δ^{13}C, ‰	±SD	Mean δ^{15}N, ‰	±SD
Benthi- and planktivorous fish	−25.77	1.08	10.26	0.91
Ichthyosaurus fish	−25.55	0.07	10.57	0.57
Insects	−25.96	1.40	4.67	0.80
Molluscs	−24.10	1.73	5.10	0.36
Carnivorous mammals	−23.12	0.82	7.79	1.89
Herbivorous mammals	−23.12	4.41	4.47	1.54
Great cormorants	−26.10		15.30	
A. flavicollis Juodkrantė (control)	−24.20	0.17	12.26	2.32
A. flavicollis Juodkrantė (colony)	−24.19	0.48	16.31	3.01
A. flavicollis Lukštas (control)	−24.89	1.25	4.06	0.71
A. flavicollis Lukštas (colony)	−25.64	0.27	5.46	0.37
A. flavicollis Zarasai (control)	−24.47	0.69	5.05	0.95
M. glareolus Juodkrantė (control)	−25.82		14.30	
M. glareolus Juodkrantė (colony)	−24.88	0.97	17.80	2.76
M. glareolus Lukštas (control)	−27.48	0.84	5.31	1.00
M. glareolus Lukštas (colony)	−26.54	0.80	10.46	3.14
M. glareolus Elektrėnai (control)	−26.02	0.79	8.86	2.91
M. glareolus Elektrėnai (colony)	−26.08	0.67	12.62	2.07
M. glareolus Zarasai (control)	−26.74	0.63	4.74	1.03

16.0 ± 1.9‰ in the forest floor and 16.4 ± 4.5‰ in plant leaves in the abandoned Isaki colony in Japan.

High nitrogen stable isotope ratios in seabird colonies have been explained by trophic enrichment and nitrogen decomposition processes (Lindeboom, 1984). As cormorants are among the top predators in the aquatic trophic web (Bostrom et al., 2012), their excreta (and tissue) are likely to be relatively high in biogens. Nitrogen decomposition processes such as mineralization and nitrification also increase the nitrogen isotopic ratio in the soil (Nadelhoffer and Fry, 1988) because of a high isotopic fractionation during the nitrification (Koba et al., 1998). Moreover, high nitrogen isotope ratios would be transferred to the plant tissues, and consequently every next higher trophic level typically would be enriched by 3.4 ± 1‰ (Post, 2002).

The stable nitrogen isotope ratios of small rodents in our study were at their highest in Juodkrantė, situated near the Baltic Sea and Curonian Lagoon. As the marine resources are enriched in both ^{15}N and ^{13}C (Hawke et al., 2013), the high stable isotope values in the hair samples are most probably due to the impact of the cormorants in the colony which fed on marine and freshwater fish and fertilized the environment with faeces with enriched nitrogen. The other cormorant colonies that were investigated at a greater distance from marine resources had a lower impact on the surrounding environment. Although not systematically investigated, *A. flavicollis* was observed feeding on the remains of the fish brought to nests (S. Paltanavičius, pers comm), as well as on dead chicks of the Great Cormorants. Similar behavior was observed in black rat (*Rattus rattus*) and house mice (*Mus musculus*) in a colony of Thin-billed Prions (*Pachyptila belcheri*) – where again a marine diet was proved to occur by using δ^{13}C and δ^{15}N isotope ratios (Quillfeldt et al., 2008). Both species also fed on Cory's Shearwater (*Calonectris diomedea borealis*) on the island ecosystem (Hervías et al., 2014).

In terms of diet, stable carbon isotopes reflect the dietary source(s) and stable nitrogen isotopes show the trophic level (Post, 2002). A wide range of carbon isotope ratios for both *A. flavicollis* and *M. glareolus* populations inhabiting the smallest and most recent colony of cormorants in Lukštas along with the control site (forest in Zarasai) suggest that carbon in these cases were assimilated from many local sources. This could reflect a wider availability of different dietary resources and abundance of the resources within different microhabitats. In contrast, the narrow ranges of carbon isotopic ratios of *A. flavicollis* and *M. glareolus* found in the largest colony site (Juodkrantė) suggest that few (dominant) food sources were utilized. This is consistent with recent studies of small mammals in Juodkrantė that showed a shift in the demographic structure of *A. flavicollis* toward males and young (Balčiauskas et al., 2015) and specific morphological features of *A. flavicollis* and *M. glareolus* (Balčiauskienė et al., 2015), both reflecting the poor habitat conditions of this site.

The small range of nitrogen isotope ratios of *A. flavicollis* in the Lukštas colony and control territory and the Zarasai control territory suggest smaller fertilization effects on the feeding sources of *A. flavicollis*, at least in Zarasai forest. It is highly unlikely that individuals captured in the Lukštas cormorant colony were recent migrants from the surrounding territories still bearing a signature of relatively low nitrogen isotope ratios, as the migration of the small mammals is limited by the position of the colony – it's surroundings are flooded (see Appendix S4). Most probably, the small colony size in Lukštas results in limited biogen pollution, hence the low values of the stable nitrogen isotope.

In the hair of *M. glareolus* from the Lukštas Great Cormorant colony, the nitrogen ratios were higher with a relatively wide range. This could be explained by the captured individuals being resident at the colony site for a relatively longer period to acquire higher nitrogen isotope ratios and by the wider trophic niche of *M. glareolus* (Butet and Delettre, 2011) enhancing their survival under harsh conditions of cormorant colony.

Similarly, the wider range of nitrogen isotopic ratios of *A. flavicollis* in Juodkrantė should indicate movement of individuals between zones with different influence by the Great Cormorants or differing time spent by mice individuals in these zones. However, as movement of *A. flavicollis* individuals between zones was not observed, it should suggest that more time spent in the zone highly affected by cormorants would give higher nitrogen isotopic ratios due to feeding on sources enriched with nitrogen.

It is known that in degraded forest ecosystems small mammals occupy higher trophic levels – disturbance leads to enrichment in of δ^{15}N in their tissues (Nakagawa et al., 2007; Darling and Bayne, 2010). A positive correlation between δ^{15}N isotope level and openness of canopy was found in omnivorous (preferring plants) small mammals, but not in insectivores (Nakagawa et al., 2007). Such findings are characteristic also to other taxa, e.g. a change of ant diet may result in an increase of the trophic position in degraded forest (Woodcock et al., 2013). In the most cormorant-affected zones, forest disruption is very high, near to total its elimination (Balčiauskas et al., 2015), and these zones are characterized also by the highest N enrichment (Adamonytė et al., 2013).

Finally, heightened δ^{15}N values in the hair of small mammals were also characteristic to the control territories of the two biggest Great Cormorant colonies (in Juodkrantė and Elektrėnai). In the case of Juodkrantė, the control territory may be biogenically polluted by birds flying over. In 2014, after measures taken to reduce the number of breeding birds, two nests were placed in the control zone, which was cormorant-free earlier. In Elektrėnai, the position of the colony on an island (see Appendix Fig. S3) and its small size supposes horizontal migration of isotopes and the possibility of animal migration between colony and control territories elsewhere on the island.

5. Conclusions

Concluding, our results showed that stable isotope ratios of dominant small mammal species differ between the ecosystems in colonies of Great Cormorants, control territories nearby (colony control) and control site far from any impact of Great Cormorants. However, we cannot exclude that small mammals in the areas highly affected by cormorants could be partially based on immigration of individuals from surrounding territories where the influence of cormorants is less or absent. Coupled with recently reported changes in the small mammal communities, populations and individual characteristics, our findings suggest an altering of the ecosystem functioning under the disturbance and biogen enrichment caused by the expansion of a Great Cormorant colony in coastal forest habitat and the transferring of biogens from the water to terrestrial ecosystem. Biogenic pollution is at its strongest in the territories of the colonies with nests, significantly diminishing in the ecotones of the colonies and further in the control zones, where the influence of birds is negligible.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.scitotenv.2016.04.185.

Ethical standards

This study was conducted in accordance with the principles of the Lithuanian legislation for animal welfare and wildlife.

Conflict of interest

The authors declare that they have no conflict of interest.

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References

Adamonytė, G., Iršėnaitė, R., Motiejūnaitė, J., Taraškevičius, R., Matulevičiūtė, D., 2013. Myxomycetes in a forest affected by great cormorant colony: a case study in Western Lithuania. Fungal Divers. 59 (1), 131–146. http://dx.doi.org/10.1007/s13225-012-0203-8.

Balčiauskas, L., Balčiauskienė, L., Jasiulionis, M., 2015. Mammals under the colony of great cormorants: population structure and body condition of the yellow-necked mice. Turkish Journal of Zoology 39 (5), 941–948. http://dx.doi.org/10.3906/zoo-1407-27.

Balčiauskienė, L., Jasiulionis, M., Balčiauskas, L., 2014. Loss of diversity in a small mammal community in a habitat influenced by a colony of great cormorants. Acta. Zool. Bulgar. 66 (2), 229–234.

Balčiauskienė, L., Balčiauskas, L., Jasiulionis, M., 2015. Skull variability of mice and voles inhabiting the territory of a great cormorant colony. Biologia 70 (10), 1406–1414. http://dx.doi.org/10.1515/biolog-2015-0152.

Bauduin, S., Cassaing, J., Issam, M., Martin, C., 2013. Interactions between the short-tailed mouse (*Mus spretus*) and the wood mouse (*Apodemus sylvaticus*): diet overlap revealed by stable isotopes. Can. J. Zool. 91 (2), 102–109. http://dx.doi.org/10.1139/cjz-2012-0286.

Bearhop, S., Adams, C.E., Waldron, S., Fuller, R.A., MacLeod, H., 2004. Determining trophic niche width: a novel approach using stable isotope analysis. J. Anim. Ecol. 73 (5), 1007–1012. http://dx.doi.org/10.1111/j.0021-8790.2004.00861.x.

Bergstrom, B.J., 2013. Would East African savanna rodents inhibit woody encroachment? Evidence from stable isotopes and microhistological analysis of feces. J. Mammal. 94 (2), 436–447. http://dx.doi.org/10.1644/12-MAMM-A-146.1.

Boecklen, W.J., Yarnes, C.T., Cook, B.A., James, A.C., 2011. On the use of stable isotopes in trophic ecology. Annu. Rev. Ecol. Evol. Syst. 42, 411–440. http://dx.doi.org/10.1146/annurev-ecolsys-102209-144726.

Bogdziewicz, M., Zwolak, R., 2014. Responses of small mammals to clear-cutting in temperate and boreal forests of Europe: a meta-analysis and review. Eur. J. For. Res. 133 (1), 1–11. http://dx.doi.org/10.1007/s10342-013-0761-7.

Bostrom, M.K., Ostman, O., Bergenius, M.A.J., Mikaela, A.J., Lunneryd, S.G., 2012. Cormorant diet in relation to temporal changes in fish communities. ICES J. Mar. Sci. 69 (2), 175–183. http://dx.doi.org/10.1093/icesjms/fss002.

Butet, A., Delettre, Y.R., 2011. Diet differentiation between European arvicoline and murine rodents. Acta Theriol. 56 (4), 297–304. http://dx.doi.org/10.1007/s13364-011-0049-6.

Caut, S., Angulo, E., Courchamp, F., 2008. Discrimination factors (Δ15N and Δ13C) in an omnivorous consumer: effect of diet isotopic ratio. Funct. Ecol. 22 (2), 255–263. http://dx.doi.org/10.1111/j.1365-2435.2007.01360.x.

Čepelka, L., Heroldová, M., Jánová, E., Suchomel, J., 2014. The dynamics of nitrogenous substances in rodent diet in a forest environment. Mammalia 78 (3), 327–333. http://dx.doi.org/10.1515/mammalia-2013-0017.

Codron, D., Sponheimer, M., Codron, J., Newton, I., Lanham, J.L., Clauss, M., 2012. The confounding effects of source isotopic heterogeneity on consumer–diet and tissue–tissue stable isotope relationships. Oecologia 169 (4), 939–953. http://dx.doi.org/10.1007/s00442-012-2274-3.

Crawford, K., Mcdonald, R.A., Bearhop, S., 2008. Applications of stable isotope techniques to the ecology of mammals. Mammal Rev. 38 (1), 87–107. http://dx.doi.org/10.1111/j.1365-2907.2008.00120.x.

Dalerum, F., Angerbjörn, A., 2005. Resolving temporal variation in vertebrate diets using naturally occurring stable isotopes. Oecologia 144 (4), 647–658. http://dx.doi.org/10.1007/s00442-005-0118-0.

Dammhahn, M., Soarimalala, V., Goodman, S.M., 2013. Trophic niche differentiation and microhabitat utilization in a species-rich montane forest small mammal community of eastern Madagascar. Biotropica 45 (1), 111–118. http://dx.doi.org/10.1111/j.1744-7429.2012.00893.x.

Darling, A.F., Bayne, E.M., 2010. The potential of stable isotope (δ^{13}C, δ^{15}N) analyses for measuring foraging behaviour of animals in disturbed boreal forest. Ecoscience 17 (1), 73–82. http://dx.doi.org/10.2980/17-1-3287

Dekker, J.J., Hofmeester, T.R., 2014. The status of the American mink (*Neovison vison*) in the Netherlands. Lutra 57 (1), 5–15.

Garbaras, A., Andriejauskienė, J., Barisevičiūtė, R., Remeikis, V., 2008. Tracing of atmospheric aerosol sources using stable carbon isotopes. Lith. J. Phys. 48 (3), 259–264. http://dx.doi.org/10.3952/lithjphys.48309.

Gehler, A., Tütken, T., Pack, A., 2012. Oxygen and carbon isotope variations in a modern rodent community – implications for palaeoenvironmental reconstructions. PLoS One 7 (11), e49531. http://dx.doi.org/10.1371/journal.pone.0049531.

Hawke, D.J., Clark, J.M., Vallance, J.R., 2013. Breeding Westland petrels as providers of detrital carbon and nitrogen for soil arthropods: a stable isotope study. J. R. Soc. N. Z. 43 (1), 58–65. http://dx.doi.org/10.1080/03036758.2011.616211.

Hervías, S., Ceia, F.R., Pipa, T., Nogales, M., de Ybáñez, R.R., Ramos, J.A., 2014. How important are seabirds in the diet of black rats on islands with a superpredator? Zoology 117 (3), 171–178. http://dx.doi.org/10.1016/j.zool.2013.12.003.

Hobara, S., Osono, T., Koba, K., Tokuchi, N., Fujiwara, S., Kameda, K., 2001. Forest floor quality and N transformations in a temperate forest affected by avian-derived N deposition. Water Air Soil Pollut. 130 (1), 679–684. http://dx.doi.org/10.1023/A:1013869115132.

Hobson, K.A., 1999. Tracing origins and migration of wildlife using stable isotopes: a review. Oecologia 120 (3), 314–326. http://dx.doi.org/10.1007/s004420050865.

Ishida, A., 1996. Effects of the common cormorant, *Phalacrocorax carbo*, on evergreen forests in two nest sites at Lake Biwa, Japan. Ecol. Res. 11 (2), 193–200. http://dx.doi.org/10.1007/BF02347685.

Kameda, K., Koba, K., Hobara, S., Osono, T., Terai, M., 2006. Pattern of natural 15N abundance in lakeside forest ecosystem affected by cormorant-derived nitrogen. Hydrobiologia 567 (1), 69–86. http://dx.doi.org/10.1007/s10750-006-0052-0.

Klimaszyk, P., Brzeg, A., Rzymski, P., Piotrowicz, R., 2015. Black spots for aquatic and terrestrial ecosystems: impact of a perennial cormorant colony on the environment. Sci. Total Environ. 517 (1), 222–231. http://dx.doi.org/10.1016/j.scitotenv.2015.02.067.

Koba, K., Tokuchi, N., Yoshioka, T., Hobbie, E.A., Iwatsubo, G., 1998. Natural abundance of nitrogen-15 in a forest soil. Soil Sci. Soc. Am. J. 62 (3), 778–781. http://dx.doi.org/10.2136/sssaj1998.03615995006200030034x.

Kolb, G.S., Jerling, L., Hambäck, P.A., 2010. The impact of cormorants on plant–arthropod food webs on their nesting islands. Ecosystems 13 (3), 353–366. http://dx.doi.org/10.1007/s10021-010-9323-8.

Kutorga, E., Iršėnaitė, R., Iznova, T., Kasparavičius, J., Markovskaja, S., Motiejūnaitė, J., 2013. Species diversity and composition of fungal communities in a Scots pine forest affected by the great cormorant colony. Acta Mycol 48 (2), 173–188. http://dx.doi.org/10.5586/am.2013.019.

Lindeboom, H.J., 1984. The nitrogen pathway in a penguin rookery. Ecology 65 (1), 269–277. http://dx.doi.org/10.2307/1939479.

Miller, J.F., Millar, J.S., Longstaffe, F.J., 2008. Carbon- and nitrogen-isotope tissue-diet discrimination and turnover rates in deer mice (*Peromyscus maniculatus*). Can. J. Zool. 86 (7), 685–691. http://dx.doi.org/10.1139/Z08-042.

Morkūnė, R., 2011. Trophic peculiarities of the Great Cormorant, Grey Heron and Long-tailed Duck on the Baltic Sea Lithuanian coast: a stable isotope approach. Ekologiia 57 (4), 173–178. http://dx.doi.org/10.6001/ekologija.v57i4.2275.

Motiejūnaitė, J., Iršėnaitė, R., Adamonytė, G., Dagys, M., Taraškevičius, R., Matulevičiūtė, D., Koreivienė, J., 2014. Pine forest lichens under eutrophication generated by a great cormorant colony. Lichenologist 46 (2), 213–228. http://dx.doi.org/10.1017/S0024282913000820.

Nadelhoffer, K.J., Fry, B., 1988. Controls on natural nitrogen-15 and carbon-13 abundances in forest soil organic matter. Soil Sci. Soc. Am. J. 52 (6), 1633–1640. http://dx.doi.org/10.2136/sssaj1988.03615995005200060024x.

Nakagawa, M., Hyodo, F., Nakashizuka, T., 2007. Effect of forest use on trophic levels of small mammals: an analysis using stable isotopes. Can. J. Zool. 85 (4), 472–478. http://dx.doi.org/10.1139/Z07-026.

Niedzialkowska, M., Konczak, J., Czarnomska, S., Jedrzejewska, B., 2010. Species diversity and abundance of small mammals in relation to forest productivity in northeast Poland. Ecoscience 17 (1), 109–119. http://dx.doi.org/10.2980/17-1-3310

O'Connell, T.C., Hedges, R.E.M., 1999. Isotopic comparison of hair and bone: archaeological analyses. J. Archaeol. Sci. 26 (6), 661–665. http://dx.doi.org/10.1006/jasc.1998.0383.

Panzacchi, M., Linnell, J.D., Melis, C., Odden, M., Odden, J., Gorini, L., Andersen, R., 2010. Effect of land-use on small mammal abundance and diversity in a forest–farmland mosaic landscape in south-eastern Norway. For. Ecol. Manag. 259 (8), 1536–1545. http://dx.doi.org/10.1016/j.foreco.2010.01.030.

Post, D.M., 2002. Using stable isotopes to estimate trophic position: models, methods and assumptions. Ecology 83, 703–718. http://dx.doi.org/10.1890/0012-9658(2002)083%5B0703:USITET%5D2.0.CO;2.

Prevedello, J.A., Dickman, C.R., Vieira, M.V., Vieira, E.M., 2013. Population responses of small mammals to food supply and predators: a global meta-analysis. J. Anim. Ecol. 82 (5), 927–936. http://dx.doi.org/10.1111/1365-2656.12072.

Quillfeldt, P., Schenk, I., McGill, R.A., Strange, I.J., Masello, J.F., Gladbach, A., Roesch, V., Furness, R.W., 2008. Introduced mammals coexist with seabirds at New Island, Falkland Islands: abundance, habitat preferences, and stable isotope analysis of diet. Polar Biol. 31 (3), 333–349. http://dx.doi.org/10.1007/s00300-007-0363-2.

Rakauskas, V., 2014. Stable isotope study of the Lake Drūkšiai food web before the Ignalina Nuclear Power Plant closure. Zool. Ecol. 24 (2), 160–167. http://dx.doi.org/10.1080/21658005.2014.925233.

Renaud, S., Michaux, J., Schmidt, D.N., Aguilar, J.P., Mein, P., Auffray, J.C., 2005. Morphological evolution, ecological diversification and climate change in rodents. Proc. R. Soc. Lond. B Biol. Sci. 272 (1563), 609–617. http://dx.doi.org/10.1098/rspb.2004.2992.

Robb, G.N., Woodborne, S., Bennett, N.C., 2012. Subterranean sympatry: an investigation into diet using stable isotope analysis. PLoS One 7 (11), e48572. http://dx.doi.org/10.1371/journal.pone.0048572.

Selva, N., Hobson, K.A., Cortés-Avizanda, A., Zalewski, A., Donázar, J.A., 2012. Mast pulses shape trophic interactions between fluctuating rodent populations in a primeval forest. PLoS One 7 (12), e51267. http://dx.doi.org/10.1371/journal.pone.0051267.

Smiley, T.M., Cotton, J.M., Badgley, C., Cerling, T.E., 2015. Small mammal isotope ecology tracks climate and vegetation gradients across western North America. Oikos http://dx.doi.org/10.1111/oik.02722 Article first published online: 9 NOV 2015.

Smith, J.J., Millar, J.S., Longstaffe, F.J., Boonstra, R., 2009. The effect of metabolic rate on stable carbon and nitrogen isotope compositions in deer mice, *Peromyscus maniculatus*. Can. J. Zool. 88 (1), 36–42. http://dx.doi.org/10.1139/Z09-116.

Sollmann, R., White, A.M., Gardner, B., Manley, P.N., 2015. Investigating the effects of forest structure on the small mammal community in frequent-fire coniferous forests using capture-recapture models for stratified populations. Mamm. Biol. - Zeitschrift für Säugetierkunde 80 (4), 247–254. http://dx.doi.org/10.1016/j.mambio.2015.03.002.

StatSoft. Inc., 2010. Electronic Statistics Textbook. StatSoft, Tulsa, OKhttp://www.statsoft.com/textbook/ accessed at: 2015.07.20.

Szpak, P., Millaire, J.F., White, C.D., Longstaffe, F.J., 2012. Influence of seabird guano and camelid dung fertilization on the nitrogen isotopic composition of field-grown maize (*Zea mays*). J. Archaeol. Sci. 39 (12), 3721–3740. http://dx.doi.org/10.1016/j.jas.2012.06.035.

Tieszen, L.L., Boutton, T.W., Tesdahl, K.G., Slade, N.A., 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: implications for δ^{13}C analysis of diet. Oecologia 57 (1), 32–37. http://dx.doi.org/10.1007/BF00379558.

Urton, E.J., Hobson, K.A., 2005. Intrapopulation variation in gray wolf isotope (δ^{15}N and δ^{13}C) profiles: implications for the ecology of individuals. Oecologia 145 (2), 316–325. http://dx.doi.org/10.1007/s00442-005-0124-2.

Van den Heuvel, I.M., Midgley, J.J., 2014. Towards an isotope ecology of Cape Fynbos small mammals. Afr. Zool. 49 (2), 195–202. http://dx.doi.org/10.3377/004.049.0208.

Vander Zanden, M.J., Clayton, M.K., Moody, E.K., Solomon, C.T., Weidel, B.C., 2015. Stable isotope turnover and half-life in animal tissues: a literature synthesis. PLoS One 10 (1), e0116182. http://dx.doi.org/10.1371/journal.pone.0116182.

Woodcock, P., Edwards, D.P., Newton, R.J., Vun, Khen C., Bottrell, S.H., Hamer, K.C., 2013. Impacts of intensive logging on the trophic organisation of ant communities in a biodiversity hotspot. PLoS One 8 (4), e60756. http://dx.doi.org/10.1371/journal.pone.0060756.

PAPER V

Immediate increase in isotopic enrichment in small mammals following the expansion of a great cormorant colony

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Immediate increase in isotopic enrichment in small mammals following the expansion of a great cormorant colony

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Abstract. Colonies of great cormorants (*Phalacrocorax carbo*) impact terrestrial ecosystems through the transport of nutrients from aquatic to terrestrial ecosystems. Deposited guano overload the ecosystem with N and P, change soil pH and damage vegetation. The ways in which small mammals are impacted, however, are little known. We aimed to evaluate the effects of an expanding great cormorant colony, testing if the expansion immediately increased the input of biogens into the forest ecosystem and, further, if the growing influence of the colony was reflected in basal resources (plants and invertebrates) and the hair of small mammals. δ^{15}N and δ^{13}C signatures were analyzed in granivorous yellow-necked mice (*Apodemus flavicollis*), omnivorous bank voles (*Myodes glareolus*) and basal resources of animal and plant origin from the territory of a colony of great cormorants situated near the Baltic Sea in west Lithuania. We found that biogens transferred by great cormorants to the terrestrial ecosystem affected the potential foods of the small mammals and led to highly elevated and variable δ^{15}N values. An increase of the size of the colony in 2015 resulted in isotopic enrichment of the small mammals in the zone of expansion in comparison to levels in 2014. The increase of δ^{15}N in *A. flavicollis* was 7.5 % ($p < 0.05$) in the ecotone and 5.7 % in the expansion zone. The decrease in δ^{13}C signatures in *A. flavicollis* was 4.5 % ($p < 0.1$) in the expansion zone and 3.1 % ($p < 0.001$) in the colony. In *M. glareolus*, the decrease in δ^{13}C signatures was 8.5 % in the expansion zone, 3.3 % ($p < 0.1$) in the control zone and 2.6 % in the ecotone. Isotopic niches (central ellipses) of *A. flavicollis* in the colony and between the control and expansion zones were separated in 2014 and 2015, while they partially overlapped in the ecotone. The isotopic niches of *M. glareolus* in 2014 and 2015 were separated in the ecotone and had a small overlap in the colony. For most of the resources tested, the isotopic signatures in the established colony area were significantly higher than in the rest of cormorant-inhabited area. In the colony, the δ^{15}N values in plants (16.9 ± 1.1 ‰) were higher than in invertebrates (13.6 ± 0.4 ‰). In the ecotone, the δ^{15}N values were 12.0 ± 1.4 in plants and 14.7 ± 0.04 ‰ in invertebrates, while in the expansion zone they were 7.2 ± 3.0 and 9.9 ± 3.8 ‰, respectively. δ^{15}N-rich resources led to increased δ^{15}N values in the hair of *A. flavicollis* and *M. glareolus*. Thus, biogens from the great cormorant colony immediately affected small mammals through their food sources.

1 Introduction

Great cormorants (*Phalacrocorax carbo*) have one of the greatest impacts on the terrestrial ecosystems of all birds breeding in colonies and transporting nutrients from aquatic to terrestrial ecosystems (Klimaszyk et al., 2015). Cormorant excreta change soil pH, N and P levels and damage vegetation (Kameda et al., 2006; Klimaszyk and Rzymski, 2016), decreasing the diversity of plants (Boutin et al., 2011) and affecting seed germination (Żółkoś and Meissner, 2008). Cormorant faeces may cover up to 80 % of vegetation, with as many as 70 % of plant species disappearing in the established colonies, the rest being dominated by nitrophilous plants, such as elder (*Sambucus nigra*), common nettle (*Urtica dioica*), woodland groundsel (*Senecio sylvaticus*) and greater celandine (*Chelidonium majus*; Goc et al., 2005; Klimaszyk et al., 2015). The abundance and diversity of herbiv-

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orous insects also decreases, while other arthropod groups may be abundant (Kolb et al., 2012).

With regard to great cormorant colonies and small mammals, investigations are scarce. In previous studies, we have discovered that the great cormorant colony in Juodkrantė, Lithuania, changes the ecology of the small mammals inhabiting the territory, decreasing their diversity and abundance (Balčiauskienė et al., 2014), as well as changing population structure and fitness (Balčiauskas et al., 2015) – these changes indicate poor habitat and heightening values of δ^{13}C and δ^{15}N in their hair (Balčiauskas et al., 2016). Unexpectedly, the number of breeding cormorant pairs in the colony increased in 2015 due to the absence of deterrent measures. Cormorants built nests in formerly uninhabited territories, giving a unique opportunity to evaluate the immediate effect of colony formation. As a bigger number of nests should be related to increased biological pollution, we hypothesized that stable isotope values will also increase in small mammal hair.

We analyzed the isotope composition in small mammal hair during the period of cormorant colony growth, comparing the isotopic signatures in samples of small mammal hair obtained in 2014 and 2015. The aim was to evaluate the effects of the transfer of biogens from the aquatic to terrestrial ecosystem by the expanding great cormorant colony. We tested (i) if the expansion of the great cormorant colony immediately increases the input of biogens to the forest ecosystem, and (ii) if the influence of the great cormorant colony is reflected in the basal resources (plants and invertebrates) and the hair of small mammals. The novelty of our investigation was in evaluating the immediacy of the impact of the great cormorant colony on small mammals. The results for the first time showed how fast biogenic pollution is transferred and what the consequences are to small mammal ecology. The immediacy of the impact of the new nests has a practical implication, specifically illustrating potential negative consequences if bird scaring is deployed and the colony moves to a new territory.

2 Material and methods

2.1 Study site

In 2015, small mammals were trapped and samples of their possible foods were collected in the territory of the biggest colony of great cormorants (*Phalacrocorax carbo*) in Lithuania (Fig. 1), situated near the settlement of Juodkrantė (WGS 55°31′14.22″ N, 21°6′37.74″ E). The colony is in Kuršių Nerija National Park, which has been a UNESCO World Heritage site since 2000.

The colony existed in the 19th century, but due to persecution disappeared in 1887. Returning only after 100 years, breeding cormorants were again registered in 1989 and thereafter the colony rapidly expanded – reaching 1000 breeding pairs by 1999 and 2800 pairs in 2004. In the same year, measures to limit breeding success at the Juodkrantė great cormorant colony were implemented (Knyva, unpublished) with the aim of limiting colony expansion. Regardless, over 3500 nests have been recorded in the colony each year since 2010, with the exception of 2014 when, due to stringent control measures (firing petards in the nesting period), the number of successful pairs was under 2000. In 2015, measures were not applied, resulting in colony growth. In that year, nests appeared in an area that had been free of cormorants in 2014 and had been used as control zone in Balčiauskas et al. (2016).

Three zones were defined for this study, namely the colony, ecotone and expansion zone. The colony included the area with the highest concentration of nests and the area of former active influence with dead trees. The ecotone (position of the trap lines shown in Fig. 1a) was situated between the colony and forest not used by cormorants (shown in darker green in Fig. 1b). Its position did not change in 2011–2014, but a small number of nests did appear in the ecotone in 2015. Also in 2015, the area of the colony expanded by about 3 ha northward (Fig. 1b), the expansion zone. Nests and droppings appeared in the zone, but trees showed no visible influence of the birds. In 2013–2014, this expansion zone was used as trapping control (Balčiauskas et al., 2015, 2016); thus we were able to compare results to find colony influence after a single year of cormorant breeding in a formerly unaffected territory

2.2 Small mammal sampling

Small mammals were trapped in September 2015, using lines of 25 snap traps placed every 5 m. The expansion and ecotone zones had two such lines each, and six lines were located in the great cormorant colony (Fig. 1a). Baited with bread and sunflower oil, the traps were left for 3 days and checked every morning. Trapping effort was equal to 750 trap days and 125 individuals were trapped. Individuals were measured, and sex and age were recorded during dissection as described elsewhere (Balčiauskas et al., 2015). The study was conducted in accordance with the principles of Lithuanian legislation for animal welfare and wildlife.

The dominant species were yellow-necked mice (*Apodemus flavicollis*) and bank voles (*Myodes glareolus*), while harvest mice (*Micromys minutus*), root voles (*Microtus oeconomus*) and short-tailed voles (*M. agrestis*) were also trapped in very low numbers. Two shrew species, common (*Sorex araneus*) and pygmy shrews (*S. minutus*), were trapped occasionally. The trapped rodent species differ in food preferences, ranging from herbivory in *Microtus* to granivory in *Apodemus* and *Micromys*, and omnivory in *Myodes* (Butet and Delettre, 2011; Čepelka et al., 2014). In general though, small mammals are mostly omnivorous (Nakagawa et al., 2007), though *Sorex* typically consume invertebrates (Makarov and Ivanter, 2016).

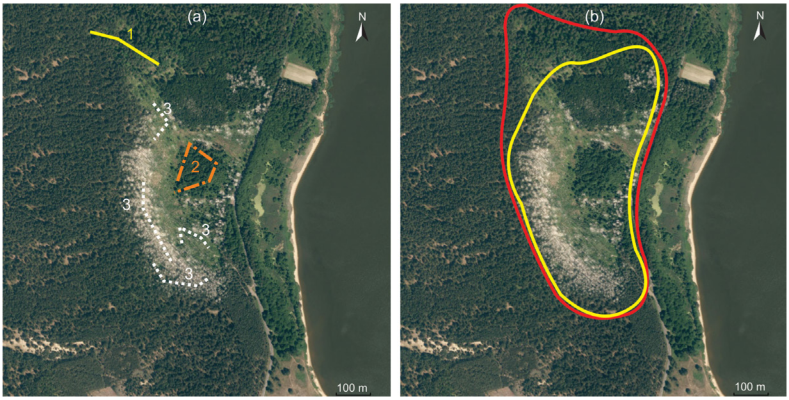

Figure 1. Trapping design in the great cormorant colony in Juodkrantė **(a)** and colony expansion in 2015 **(b)**. **(a)** Position of the trap lines in 2015: 1 – expansion, 2 – ecotone, 3 – the colony. **(b)** Yellow line – colony area in 2014, red line – colony expansion in 2015.

Table 1. Numbers of trapped individuals of the two dominant small mammal species in the Juodkrantė great cormorant colony in 2014 (before colony expansion) and in 2015 (the year colony expanded).

	Apodemus flavicollis			*Myodes glareolus*		
Year	Control/ expansion*	Ecotone	Colony	Control/ expansion	Ecotone	Colony
2014	13	28	64	1	7	25
2015	17	33	43	2	20	8

* Control zone in 2014 became expansion zone in 2015.

The numbers of rodents trapped in the different zones of the territory (control/expansion, ecotone and the colony itself) in 2014 and 2015 are presented in Table 1, while the age and sex composition of the two dominant species in 2015 are shown in Table S1. No small mammals were trapped in the areas of the great cormorant colony that contained the highest concentration of nests and had experienced long-term influence. In the expansion part of the colony, only *A. flavicollis* was trapped in significant numbers in 2015.

2.3 Baseline sampling

Isotopic signatures were evaluated and isotopic baselines were established from possible dietary items. In 2015, we collected samples of the possible food items at the locations where the small mammals were trapped or at the closest available place. In the most affected zones, plant diversity was extremely restricted, with just a few nitrophilous species present. In total, 45 plant and 9 invertebrate samples were collected. Five litter samples and seven samples of great cormorant feathers and eggshells were also collected.

Plant samples included leaves of greater celandine (*Chelidonium majus*), sedges (*Carex* sp.), raspberry (*Rubus idaeus*), rush (*Juncus* sp.), blackberry (*Rubus fruticosus*) and bilberry (*Vaccinium myrtillus*), leaves and berries of elder (*Sambucus nigra*), alder buckthorn (*Rhamnus frangula*) and European barberry (*Berberis vulgaris*), and oak (*Quercus robur*) acorns. Invertebrate samples included coprophagous dung beetle (*Geotrupes stercorarius*), herbivorous dark bush-cricket (*Pholidoptera griseoaptera*), predatory ground beetle (*Carabus* sp.) and omnivorous land slug (*Deroceras* sp.). Quantifying of the different foods by volume was not done. Unfortunately, we have no data on the isotopic signatures in basal resources from the pre-expansion period in 2014.

2.4 Stable isotope analysis

We used the hair of the rodents as metabolically inert samples, these preserving the isotopic record of the animal's diet (Crawford et al., 2008; Bauduin et al., 2013). Hair samples were taken with scissors from between the shoulders of most of the trapped specimens of *A. flavicollis* and *M. glareolus* (88 and 29 individuals; see Table S1 in the Supplement). Individuals contaminated by fly larvae or predators were not sampled for stable isotopes. Each sample was placed separately in a bag and stored dry. Samples were weighed with a microbalance and packed in tin capsules. As few individuals of these species survive longer than 1 year, with most overwintering individuals being autumn born (Bobek, 1969), our samples thus represent the influence of the cormorants in the year that the rodents were trapped.

Environmental samples (including plants, litter, invertebrates and great cormorant feathers and eggs) were stored in a freezer at below −20 °C prior to preparation and analysis. Samples were dried in an oven at 60 °C to a constant weight for 24–48 h and then homogenized to a fine powder (using mortar and pestle and a Retsch mixer mill MM 400). Pretreatment of hair and other samples was not done, as after testing it produced no change of results. Feathers were cleaned with acetone and deionized water prior to measurements. Feather samples were clipped from the vane avoiding the rachis.

Stable isotope ratios (δ^{13}C and δ^{15}N) were measured using an elemental analyzer (EA) coupled to an isotope ratio mass spectrometer (Flash EA1112; Thermo Delta V Advantage, Thermo Scientific, USA). Stable isotope data are reported as δ values, according to the formula $\delta X = [R_{\mathrm{sample}}/R_{\mathrm{standard}} - 1] \times 10^3$, where $R_{\mathrm{sample}} = {}^{13}\mathrm{C}/{}^{12}\mathrm{C}$ or ${}^{15}\mathrm{N}/{}^{14}\mathrm{N}$ of the sample, $R_{\mathrm{standard}} = {}^{13}\mathrm{C}/{}^{12}\mathrm{C}$ or ${}^{15}\mathrm{N}/{}^{14}\mathrm{N}$ of the standard.

5 % of samples were run in duplicate. The equipment parameters and measurement quality control are detailed elsewhere (Balčiauskas et al., 2016).

2.5 Statistical analysis

The normality of distribution of δ^{13}C and δ^{15}N values was tested using the Kolmogorov–Smirnov D. As not all values of δ^{13}C and δ^{15}N were distributed normally, the influences of species and the zone of the colony on the carbon and nitrogen stable isotope values in the mammal hair were tested using nonparametric Kruskal–Wallis ANOVA. Independent groups were compared with the same Kruskal–Wallis multiple comparisons procedure (StatSoft, 2013). Differences in δ^{13}C and δ^{15}N ratios between 2014 (data from Balčiauskas et al., 2016) and 2015 were tested by multivariate Hotelling T^2 test. The minimum significance level was set at $p < 0.05$. Calculations were performed using Statistica for Windows, version 6.0.

Environmental samples were analyzed by object group (cormorant, litter, invertebrates, plants) and by the zone (expansion, ecotone, colony). Isotopic baselines were calculated using basal resources as possible foods for rodents grouped according to their origin. Reported values are arithmetic means with SE of the δ^{15}N and δ^{13}C for all basal resources mentioned above.

The isotopic niches of species, as central ellipses, were calculated using SIBER (Jackson et al., 2011) under R version 3.5.0 (https://cran.r-project.org/bin/windows/base/rdevel.html, last access: 2 June 2018) for *A. flavicollis* and *M. glareolus* in the zones, where five or more individuals were investigated for δ^{15}N and δ^{13}C.

3 Results

3.1 δ^{13}C and δ^{15}N values in the hair of small mammals inhabiting the great cormorant colony

The distribution of both δ^{13}C and δ^{15}N values in the hair of *A. flavicollis* and the distribution of δ^{15}N values in *M. glareolus* were not normal, though the distribution δ^{13}C in *M. glareolus* values corresponded to normal. Outliers from the normal distribution were values registered in the expansion zone (Fig. S1 in the Supplement). Kruskal–Wallis ANOVA demonstrated that the distribution of stable isotope values was influenced not only by zone, but also by the species of small mammal. These factors together significantly influenced the distribution of δ^{15}N ($r^2 = 0.31$) and δ^{13}C ($r^2 = 0.26$, F both $p < 0.0001$).

Table 2. Central position (mean ± SE, ‰) of stable isotope ratios in the hair of *Apodemus flavicollis* and *Myodes glareolus* trapped in the Juodkrantė colony of great cormorants. Data for 2014 recalculated from Balčiauskas et al. (2016). Significance of differences according to the Hotelling T^2 multivariate test, * $p < 0.1$, ** $p < 0.05$, *** $p < 0.001$.

Species	Zone	Year	δ^{13}C, ‰ ± SE	δ^{15}N, ‰ ± SE
Apodemus flavicollis	Control	2014	−24.20 ± 0.08	12.26 ± 1.04
	Expansion	2015	−25.30 ± 0.33*	12.96 ± 0.94
	Ecotone	2014	−24.37 ± 0.13	15.97 ± 0.45
		2015	−24.51 ± 0.10	17.16 ± 0.26**
	Colony	2014	−24.08 ± 0.12***	16.52 ± 0.90
		2015	−24.82 ± 0.12	16.67 ± 0.50
Myodes glareolus	Control	2014	−25.82	14.30
	Expansion	2015	−28.02 ± 0.85	6.70 ± 0.91
	Ecotone	2014	−24.85 ± 0.30	17.48 ± 0.64
		2015	−25.49 ± 0.16	17.87 ± 0.30
	Colony	2014	−24.89 ± 0.31*	17.99 ± 0.91
		2015	−25.72 ± 0.17	18.17 ± 0.26

In 2015, the influence of the zone (both species pooled) was significant for the distribution of δ^{15}N (Kruskal–Wallis ANOVA, $\mathrm{H}_{2,119} = 18.62$, $p = 0.0001$) and δ^{13}C ($\mathrm{H}_{2,119} = 6.30$, $p = 0.043$). Between-species differences in the stable isotope values in the hair of the rodents in the colony area were highly significant for δ^{13}C ($\mathrm{H}_{1,119} = 21.69$, $p < 0.0001$) and for δ^{15}N ($\mathrm{H}_{1,119} = 6.67$, $p = 0.01$). δ^{15}N values were highest in the hair of *M. glareolus* trapped in the ecotone and colony zones, while highest in *A. flavicollis* in the expansion zone. δ^{13}C signatures in the hair of *A. flavicollis* were higher than in *M. glareolus* in all territories, including the expansion zone (Table 2).

With the expansion of the great cormorant colony in 2015, the isotopic signatures of δ^{15}N in dominant small mammal hair grew in comparison to 2014, though not all differences are significant (Table 2). In *A. flavicollis,* δ^{15}N values increased in all zones (the 7.5 % increase in the ecotone zone is significant at $p < 0.05$). The increase in the colony was ∼ 1 %, while the expansion zone compared to former control zone was 5.7 %. All are correlated with colony growth and expansion. In *M. glareolus*, δ^{15}N increased by 2.3 % in the ecotone zone and ∼ 1 % in the colony.

δ^{13}C signatures in the hair of *A. flavicollis* in 2015 decreased in all zones. The decrease in the expansion zone compared to 2014 control zone was 4.5 % ($p < 0.1$), in the colony zone 3.1 % ($p < 0.001$) and in the ecotone zone 0.5 %. In the hair of *M. glareolus*, the decrease of δ^{13}C signatures was even stronger – 8.5 % in the expansion zone, 3.3 % ($p < 0.1$) in the control zone and 2.6 % in the ecotone (Table 2). We suppose that no other factor other than colony growth could account for these changes.

Isotopic niches of *A. flavicollis* in 2014 and 2015 (shown as central ellipses) were separated in the colony and between the control and expansion zones, while they partially overlapped in the ecotone (Fig. S2a). The isotopic niches of *M. glareolus* in 2014 and 2015 were separated in the ecotone and had a small overlap in the colony (Fig. S2b). Insufficient sample size did not allow analysis in the control and expansion zones for this species (see Table 1).

3.2 Basal resources

Comparing average baseline data of plants and invertebrates between the expansion zone, ecotone and colony (Table 3), considerable differences were noted in the δ^{15}N of plants (Kruskal–Wallis ANOVA, $H_{2,45} = 13.89$, $p = 0.001$) but not in invertebrates ($H_{2,9} = 2.76$, $p = 0.25$). In plants, δ^{15}N values were highest in the colony (difference from expansion zone, $p < 0.002$; difference from ecotone, $p = 0.062$). δ^{13}C values showed no significant differences between zones in either plants or invertebrates (Table 3).

Out of ten plant species, the most ^{15}N enriched were as follows: *Chelidonium majus*, $\delta^{15}\text{N} = 19.6 \pm 2.0$ ‰ (from 8.4 in the expansion zone to 25.7 ‰ in the colony); *Sambucus nigra*, $\delta^{15}\text{N} = 16.9 \pm 2.6$ ‰ (from 9.2 in the ecotone to 22.5 ‰ in the colony); *Juncus* sp., $\delta^{15}\text{N} = 13.8 \pm 4.7$ ‰; and *Rhamnus frangula*, $\delta^{15}\text{N} = 13.2 \pm 1.8$ ‰ (from 8.1 ‰ in the expansion zone to 16.3 ‰ in the colony). δ^{15}N values in *Carex* sp. (average $\delta^{15}\text{N} = 12.3 \pm 0.9$ ‰) did not differ significantly across zones.

The most δ^{13}C-enriched plants were *Carex* sp. with $\delta^{13}\text{C} = -26.7 \pm 0.7$ ‰ and *Sambucus nigra* with $\delta^{13}\text{C} = -27.5 \pm 0.6$ ‰, values in the expansion zone and colony did not differ. *Chelidonium majus* was among the least δ^{13}C-enriched plants, $\delta^{13}\text{C} = -29.5 \pm 0.4$ ‰.

Of the investigated invertebrates, the most δ^{15}N enriched were *Carabus* sp. and slugs, $\delta^{15}\text{N} = 14.9$ and 14.0 ‰, respectively. Dung beetles showed the highest variation of δ^{15}N, being 2 times lower in the expansion zone than in the colony (6.2 ‰ versus 13.3 ‰). The stable carbon isotope ratio in slugs was about 1 ‰ higher than in arthropods.

δ^{15}N values in the litter were highest in the colony ($\delta^{15}\text{N} = 16.3$ ‰), followed by the ecotone and expansion zones ($\delta^{15}\text{N} = 8.2$ and 7.3 ‰, respectively). δ^{15}N values in the cormorant eggshells and feathers were lower than in rodent hair and did not depend on zone (Fig. S3).

3.3 Comparison of isotopic signatures in the hair of small mammals and in possible diet resources

Comparison of isotopic signatures in the hair of *A. flavicollis* and *M. glareolus* with baseline δ^{13}C and δ^{15}N values in possible food sources from the expansion, ecotone and colony zones showed that noted differences were related to bird influence.

In the expansion and ecotone zones, invertebrate isotopic signatures were higher than in plants in terms of both δ^{13}C and δ^{15}N. In the great cormorant colony, most plants were highly enriched in ^{15}N due to over-enrichment and tended to have δ^{15}N values well above the invertebrate δ^{15}N range (Fig. 2).

Compared to average plant and invertebrate baseline values, the higher average δ^{15}N and δ^{13}C values in the hair of *A. flavicollis* and *M. glareolus* were related to the zones where the rodents were trapped (Table 4). For *A. flavicollis* trapped in the expansion and ecotone zones, the average δ^{15}N was over 5 ‰ higher than the plant baseline, but the plant baseline in the colony was higher than the δ^{15}N value in the hair. Compared to the invertebrate baseline, enrichment of ^{15}N in the rodent hair was 2.5–3 ‰. Concerning *M. glareolus*, ^{15}N enrichment was highest in the ecotone when compared to the plant baseline, but highest in the colony zone when compared to the invertebrate baseline. As for ^{13}C, enrichment was highest in the ecotone zone for both *A. flavicollis* and *M. glareolus* (Table 4).

4 Discussion

4.1 Immediacy of the great cormorant colony impact

Our main finding showed that great cormorants influenced small mammals in the very first year of the appearance of breeding colony, and possible food objects (plants and invertebrates) also were subjected to increased δ^{15}N and decreased δ^{13}C concentrations. Moreover, in 2015 – the year of colony increase and expansion – we found that the increased influence of the great cormorant colony already limited small mammal distribution. Small mammals were not trapped in the area with the highest concentration of nests. By contrast, representatives of three small mammal species had been trapped in the same place in earlier years when the number of nests was lower due to scaring measures. In the expansion part of the colony, a single individual of *M. glareolus* was trapped in 2015, while only a single species, *A. flavicollis,* was trapped in significant numbers. In 2014, before colony expansion, four small mammal species were trapped in the same area.

Table 3. Isotopic signatures of basal resources (plants and invertebrates) in the Juodkrantė great cormorant colony, ecotone and expansion zones in 2015.

Basal resources	Zone	*n*	δ^{13}C, ‰ ± SE	δ^{13}C, ‰ min–max	δ^{15}N, ‰ ± SE	δ^{15}N, ‰ min–max
Plants	Expansion	9	−28.6 ± 0.9	−32.8 to −25.2	7.2 ± 3.0	−3.3–25.1
	Ecotone	10	−29.1 ± 0.7	−31.6 to −25.2	12.0 ± 1.4	8.0–22.5
	Colony	26	−28.1 ± 0.3	−31.4 to −25.2	16.9 ± 1.1	8.4–27.7
Invertebrates	Expansion	2	−28.3 ± 0.8	−29.1 to −27.5	9.9 ± 3.8	6.2–13.7
	Ecotone	2	−26.9 ± 0.1	−26.9 to −26.8	14.7 ± 0.0	14.6–14.7
	Colony	5	−27.6 ± 0.3	−28.4 to −26.5	13.6 ± 0.4	12.8–14.9

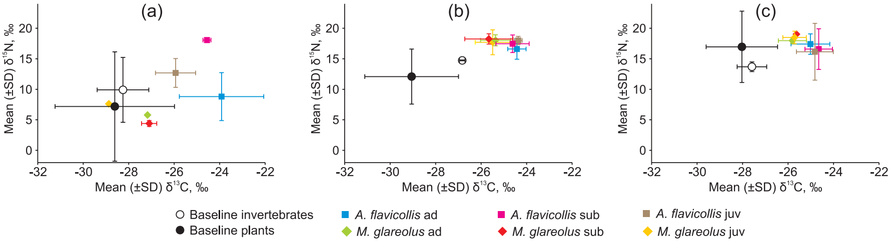

Figure 2. Isotopic signatures of potential animal and plant foods compared with isotopic signatures in the hair of age groups of *Apodemus flavicollis* and *Myodes glareolus*, trapped in the expansion **(a)** and ecotone **(b)** zones and Juodkrantė great cormorant colony **(c)** in 2015. Ad – adults, sub – subadult animals, juv – juveniles.

4.2 Biogenic pollution disclosed by stable isotope concentration in the hair of small mammals

Investigations into the influence of great cormorant colonies have recently received more attention (see Ishida, 1996; Goc et al., 2005; Kameda et al., 2006; Nakamura et al., 2010; Klimaszyk et al., 2015; Klimaszyk and Rzymski, 2016). However, the impact of such colonies on plant and animal species has not been sufficiently investigated (see Bostrom et al., 2012; Kolb et al., 2012). Small mammal ecology in the colonies was recently investigated for the first time in Lithuania (Balčiauskienė et al., 2014; Balčiauskas et al., 2015) and some aspects of isotopic enrichment of small mammals in great cormorant colonies were reviewed in Balčiauskas et al. (2016). We found that biogenic pollution resulting from the birds reach the dominant species of small mammals. Stable isotope ratios in their hair depend on the degree of cormorant influence, being strongest in the area with cormorant nests (see data in Table 2) and also on the colony size. However, we had no data regarding stable isotopes in basal resources and we were not aware how fast the influence could be.

4.3 Stable isotopes showing small mammal diet differences in various zones of cormorant colony

Stable isotope analysis (SIA) can be used to investigate the trophic structure of food webs and various aspects of animal diet (Boecklen et al., 2011; Koike et al., 2016). SIA using mammal hair is a method suitable for diet analysis and for comparing intrapopulation groups as well as different species. When analyzing diet, hair isotopic signatures are compared with the signatures of possible food sources (Bauduin et al., 2013). In identifying diet sources, carbon and nitrogen isotope ratios are most widely used. The tissues of animals do differ in isotopic composition as a result of differences in their diet. Nitrogen values help in identifying the trophic position, since these values increase by 3–5 ‰ between levels of the food chain (Kelly, 2000; Smiley et al., 2016). The stable isotope ratio in the hair reflects the dietary isotope composition and trophic level, depending on the ingested food (Cassaing et al., 2007).

As the hair of the rodents trapped in the Juodkrantė colony, ecotone and expansion zone differed in δ^{15}N and δ^{13}C values, rodents obviously consumed foods with different isotopic signatures, the more diverse diet being in the expansion zone as reflected by much higher variance of δ^{13}C values. Enrichment of plants and invertebrates was strongest in the territory of the colony (see Fig. 2).

Table 4. Nitrogen ($\Delta\delta^{15}N$) and carbon ($\Delta\delta^{13}C$) trophic fractionation between *Apodemus flavicollis* and *Myodes glareolus* and their possible food sources in the Juodkrantė great cormorant colony.

		$\Delta\delta^{15}N$, ‰		$\Delta\delta^{13}C$, ‰	
Zone	Baseline for comparison	*A. flavicollis*	*M. glareolus*	*A. flavicollis*	*M. glareolus*
Expansion	Plants	5.78	−0.48	3.31	0.59
	Invertebrates	3.05	−3.21	2.95	0.23
Ecotone	Plants	5.15	5.86	4.58	3.60
	Invertebrates	2.49	3.20	2.34	1.37
Colony	Plants	−0.23	1.27	3.32	2.41
	Invertebrates	3.11	4.61	2.76	1.86

Species-related differences in the isotopic signatures of the two dominant rodent species may be explained by diet differences and microhabitat use, both supporting coexistence (Stenseth et al., 2002; Cassaing et al., 2013). Previous experience with live-trapping and marking of *A. flavicollis* in the cormorant colony (Jasiulionis, unpublished) allowed us to conclude that movement between zones was very limited: we did not find any marked animals using multiple zones during the same year. In the resource-scarce territory of the great cormorant colony, any spatial segregation could lead to changes in the diet of the rodents. Considering the isotopic signatures in the hair of the small mammals as dietary proxies (according to Fernandes et al., 2014) reflecting the proteins of the food sources (Perkins et al., 2014), we found that diets differed in the various zones of the colony and also depended on the small mammal species. Therefore, differential exploitation of resources minimized competition (according Bauduin et al., 2013).

4.4 Pathways of small mammal enrichment in stable isotopes

There is a slight possibility that the observed rodent enrichment in $\delta^{15}N$ was a result of eating cormorant tissues. Dead chicks, broken eggs and eggshells are constantly present on the ground underneath the nests in the breeding season, and so could serve as food source. Moreover, $\delta^{15}N$ values in great cormorant eggshells and feathers were lower than the $\delta^{15}N$ values in the hair of rodents from the same zone (see Fig. S2). Furthermore, there are observations of *Microtus* and *Myodes* voles eating auklets' eggs and chicks (Drever et al., 2000). In our case however, the difference in $\delta^{15}N$ values between the cormorants and rodents was not great, questioning the possibility of consumption of cormorant tissue in any significant amount. Thus we support the opinion of Millus and Stapp (2008), that cormorant influence on small mammals is not direct, but is mediated through influence on their food resources.

The two possible pathways of marine nitrogen are (1) through guano-fertilized plants or (2) invertebrates that have fed on guano, guano-fertilized plants or cormorant remains (Harper, 2007). According to Szpak et al. (2012), ^{15}N enrichment of plants may range from 11.3 to 20 ‰ after fertilization by guano of seabirds. Plants enriched in guano ^{15}N may occur at distances exceeding 100 m from nesting sites and colonies (Millus and Stapp, 2008). A few plant samples (*Carex* and *Sambucus*) were highly enriched in ^{15}N in the expansion zone of Juodkrantė colony in 2015, the first year of the presence of cormorant nests.

Rodents usually eat foods that are most abundant (Bauduin et al., 2013) or have preferences characteristic to the species (Fisher and Türke, 2016; Schneider et al., 2017). However, choices in the Juodkrantė great cormorant colony are limited to several plant species (mainly nitrophilous) and invertebrates. Nitrophilous plants usually grow abundantly, being the food source for herbivores living in the territory of a colony (Cassaing et al., 2007). Even after birds cease to use a territory, the isotopic signatures of the litter and plants remain high (Kameda et al., 2006). Enrichment of plants by ^{15}N is a result of uptake of nitrogen from bio-polluted soil enriched by marine-derived N from great cormorant excreta. In such a situation, $\delta^{15}N$ is not a straightforward indicator of the trophic level (Drever at al., 2000). On seabird islands, herbivores often exhibit heightened $\delta^{15}N$ signatures (Stapp et al., 1999; Drever et al., 2000).

Typically, diet–tissue fractionation is from 2.5 to 3.4 ‰ for nitrogen (Perkins et al., 2014). Trophic fractionation from 3 to 5 ‰ for nitrogen occurs at every trophic level in seabird colonies (Cassaing et al., 2007). However, in Juodkrantė, it may exceed 5 ‰ in comparison to plants. Trophic fractionation for carbon of *A. flavicollis* was at a predictable level, up to 4.6 ‰ in comparison to plants, and up to 3 ‰, compared to the invertebrate baseline. Enrichment in ^{13}C of *M. glareolus* was lower, up to 3.6 ‰ compared to plants and up to 1.9 ‰, compared to the invertebrate baseline (see Table 4). These values are similar to or even higher than those observed by Sponheimer et al. (2003), with a mean diet–hair fractionation of +3.2 ‰ and a range of +2.7 to +3.5 ‰ in mammalian herbivores.

5 Conclusions

This study seeks to understand how the influence of biological pollution from the great cormorant colony reaches small mammals and how fast this influence is registered after birds appear in the territory. The general conclusion is that in Juodkrantė, Lithuania, the great cormorant colony affected the terrestrial ecosystem starting from the autotrophs and ending with the consumers (two species of rodents). An increase in the number of breeding pairs in 2015 led to increased δ^{15}N and decreased δ^{13}C values in the hair of *Apodemus flavicollis* in the territory of the colony, ecotone and expansion zone. In the expansion zone, the influence was visible after a single year of nest appearance. In the resource-limited territory under the great cormorant nests, differences in isotopic signatures were related to the species of rodent, pointing to differences in their diet. We conclude that the influence of the nutrient transport from water to land ecosystems by great cormorants is indirect, resulting from the biological pollution of guano on rodent foods. Our results show that scaring cormorants from colonies may have a negative consequence – displaced birds may build their nest in other habitats and, as such, a negative impact of an emerging new colony could spread through the entire ecosystem and impact small mammals in the first year. The immediacy of the impact from new nests has practical implications, indicating the potential benefit of deterring birds from the nests during the actual breeding period as a management measure to limit growth in numbers, rather than scaring them before breeding, which may result in colony fragmentation and the moving to new territories.

Data availability. Data used in this paper are available upon request from the corresponding author.

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Author contributions. MJ, LiB and LaB trapped small mammals and collected baseline data. MJ and RS analyzed stable isotopes. LiB analyzed data statistically. LiB and LaB wrote the first draft. All authors provided substantial input to the design of the study and discussion of the results.

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References

Balčiauskas, L., Balčiauskienė, L., and Jasiulionis, M.: Mammals under the colony of great cormorants: population structure and body condition of the yellow-necked mice, Turk. J. Zool., 39, 941–948, https://doi.org/10.3906/zoo-1407-27, 2015.

Balčiauskas, L., Skipitytė, R., Jasiulionis, M., Trakimas, G., Balčiauskienė, L., and Remeikis, V.: The impact of Great Cormorants on biogenic pollution of land ecosystems: Stable isotope signatures in small mammals, Sci. Total Environ., 565, 376–383, https://doi.org/10.1016/j.scitotenv.2016.04.185, 2016.

Balčiauskienė, L., Jasiulionis, M., and Balčiauskas, L.: Loss of Diversity in a Small Mammal Community in a Habitat Influenced by a Colony of Great Cormorants, Acta Zool. Bulgar., 66, 229–234, 2014.

Bauduin, S., Cassaing, J., Issam, M., and Martin, C.: Interactions between the short-tailed mouse (Mus spretus) and the wood mouse (Apodemus sylvaticus): diet overlap revealed by stable isotopes, Can. J. Zool., 91, 102–109, https://doi.org/10.1139/cjz-2012-0286, 2013.

Bobek, B.: Survival, turnover and production of small rodents in a beech forest, Acta Theriol., 14, 191–210, https://doi.org/10.4098/AT.arch.69-15, 1969.

Boecklen, W. J., Yarnes, C. T., Cook, B. A., and James, A. C.: On the use of stable isotopes in trophic ecology, Annu. Rev. Ecol. Evol. S., 42, 411–440, https://doi.org/10.1146/annurev-ecolsys-102209-144726, 2011.

Bostrom, M. K., Ostman, O., Bergenius, M. A. J., Mikaela, A. J., and Lunneryd, S. G.: Cormorant diet in relation to temporal changes in fish communities, ICES J. Mar. Sci., 69, 175–183, https://doi.org/10.1093/icesjms/fss002, 2012.

Boutin, C., Dobbie, T., Carpenter, D., and Hebert, C. E.: Effect of Double Crested Cormorant on island vegetation, seedbank and soil chemistry: evaluating island restoration potential, Restor. Ecol., 19, 720–727, https://doi.org/10.1111/j.1526-100X.2010.00769.x, 2011.

Butet, A. and Delettre, Y. R.: Diet differentiation between European arvicoline and murine rodents, Acta Theriol., 56, 297–304, https://doi.org/10.1007/s13364-011-0049-6, 2011.

Cassaing, J., Derré, C., Moussa, I., and Cheylan, G.: Diet variability of Mediterranean insular populations of Rattus rattus studied by stable isotope analysis, Isot. Environ. Healt. S., 43, 197–213, https://doi.org/10.1080/10256010701562919, 2007.

Cassaing, J., Riviere, B. L. P. D. L., Donno, F. D., Marlinez-Garcia, E., and Thomas, C.: Interactions between 2 Mediterranean rodent species: Habitat overlap and use of heterospecific cues, Ecoscience, 20, 137–147, https://doi.org/10.2980/20-2-3560, 2013.

Čepelka, L., Heroldová, M., Jánová, E., and Suchomel, J.: The dynamics of nitrogenous substances in rodent diet in a forest environment, Mammalia, 78, 327–333, https://doi.org/10.1515/mammalia-2013-0017, 2014.

Crawford, K., Mcdonald, R. A., and Bearhop, S.: Applications of stable isotope techniques to the ecology of mammals, Mammal Rev., 38, 87–107, https://doi.org/10.1111/j.1365-2907.2008.00120.x, 2008.

Drever, M. C., Blight, L. K., Hobson, K. A., and Bertram, D. F.: Predation on seabird eggs by Keen's mice (Peromyscus keeni): using stable isotopes to decipher the diet of a terrestrial omnivore on a remote offshore island, Can. J. Zool., 78, 2010–2018, 2000.

Fernandes, R., Millard, A. R., Brabec, M., Nadeau, M. J., and Grootes, P.: Food reconstruction using isotopic transferred signals (FRUITS): a Bayesian model for diet reconstruction, PloS One, 9, e87436, https://doi.org/10.1371/journal.pone.0087436, 2014.

Fischer, C. and Türke, M.: Seed preferences by rodents in the agri-environment and implications for biological weed control, Ecol. Evol., 6, 5796–5807, https://doi.org/10.1002/ece3.2329, 2016.

Goc, M., Iliszko, L., and Stempniewicz, L.: The largest European colony of great cormorant on the Vistula spit (N Poland)—an impact of the forest ecosystem, Ecological Questions, 6, 93–103, 2005.

Harper, G. A.: Detecting predation of a burrow-nesting seabird by two introduced predators, using stable isotopes, dietary analysis and experimental removals, Wildlife Res., 34, 443–453, https://doi.org/10.1071/WR07037, 2007.

Ishida, A.: Effects of the common cormorant, Phalacrocorax carbo, on overgreen forests in two nest sites at Lake Biwa, Japan, Ecol. Res., 11, 193–200, https://doi.org/10.1007/BF02347685, 1996.

Jackson, A. L., Inger, R., Parnell, A. C., and Bearhop, S.: Comparing isotopic niche widths among and within communities: SIBER–Stable Isotope Bayesian Ellipses in R, J. Anim. Ecol., 80, 595–602, https://doi.org/10.1111/j.1365-2656.2011.01806.x, 2011.

Kameda, K., Koba, K., Hobara, S., Osono, T., and Terai, M.: Pattern of natural ^{15}N abundance in lakeside forest ecosystem affected by cormorant-derived nitrogen, Hydrobiologia, 567, 69–86, https://doi.org/10.1007/s10750-006-0052-0, 2006.

Kelly, J. F.: Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology, Can. J. Zool., 78, 1–27, https://doi.org/10.1139/z99-165, 2000.

Klimaszyk, P. and Rzymski, P.: The complexity of ecological impacts induced by great cormorants, Hydrobiologia, 771, 13–30, https://doi.org/10.1007/s10750-015-2618-1, 2016.

Klimaszyk, P., Brzeg, A., Rzymski, P., and Piotrowicz, R.: Black spots for aquatic and terrestrial ecosystems: impact of a perennial cormorant colony on the environment, Sci. Total Environ., 517, 222–231, https://doi.org/10.1016/j.scitotenv.2015.02.067, 2015.

Koike, S., Nakashita, R., Kozakai, C., Nakajima, A., Nemoto, Y., and Yamazaki, K.: Baseline characterization of the diet and stable isotope signatures of bears that consume natural foods in central Japan, Eur. J. Wildlife Res., 62, 23–31, https://doi.org/10.1007/s10344-015-0969-6, 2016.

Kolb, G., Jerling, L., Essenberg, C., Palmborg, C., and Hambäck, P. A.: The impact of nesting cormorants on plant and arthropod diversity, Ecography, 35, 726–740, https://doi.org/10.1111/j.1600-0587.2011.06808.x, 2012.

Makarov, A. M. and Ivanter, E. V.: Dimensional characteristics of prey and their role in the diet of shrews (Sorex L.), Russ. J. Ecol., 47, 315–319, https://doi.org/10.1134/S1067413616030073, 2016.

Millus, S. A. and Stapp, P.: Interactions between seabirds and endemic deer mouse populations on Santa Barbara Island, California, Can. J. Zool., 86, 1031–1041, https://doi.org/10.1139/Z08-081, 2008.

Nakagawa, M., Hyodo, F., and Nakashizuka, T.: Effect of forest use on trophic levels of small mammals: an analysis using stable isotopes, Can. J. Zool., 85, 472–478, https://doi.org/10.1139/Z07-026, 2007.

Nakamura, M., Yabe, T., Ishii, Y., Kido, K., and Aizaki, M.: Extreme eutrophication in a small pond adjacent to a forest colonized by great cormorant (Phalacrocorax carbo), Jap. J. Limnol., 71, 19–26, https://doi.org/10.3739/rikusui.71.19, 2010.

Perkins, M. J., McDonald, R. A., van Veen, F. F., Kelly, S. D., Rees, G., and Bearhop, S.: Application of nitrogen and carbon stable isotopes (δ^{15}N and δ^{13}C) to quantify food chain length and trophic structure, PloS One, 9, e93281, https://doi.org/10.1371/journal.pone.0093281, 2014.

Schneider, S., Steeves, R., Newmaster, S., and MacDougall, A. S.: Selective plant foraging and the top-down suppression of native diversity in a restored prairie, J. Appl. Ecol., 54, 1496–1504, https://doi.org/10.1111/1365-2664.12886, 2017.

Smiley, T. M., Cotton, J. M., Badgley, C., and Cerling, T. E.: Small-mammal isotope ecology tracks climate and vegetation gradients across western North America, Oikos, 125, 1100–1109, https://doi.org/10.1111/oik.02722, 2016.

Sponheimer, M., Robinson, T., Ayliffe, L., Passey, B., Roeder, B., Shipley, L., Lopez, E., Cerling, T., Dearing, D., and Ehleringer, J.: An experimental study of carbon-isotope fractionation between diet, hair, and feces of mammalian herbivores, Can. J. Zool., 81, 871–876, https://doi.org/10.1139/z03-066, 2003.

Stapp, P., Polis, G. A., and Piñero, F. S.: Stable isotopes reveal strong marine and El Nino effects on island food webs, Nature, 401, 467–469, https://doi.org/10.1038/46769, 1999.

StatSoft, Inc.: Electronic Statistics Textbook, available at: http://www.statsoft.com/textbook/ (last access: 20 July 2017), 2013.

Stenseth, N. C., Vljugrein, H., Jędrzejewski, W., Mysterud, A., and Pucek, Z.: Population dynamics of Clethrionomys glareolus and Apodemus flavicollis: seasonal components of density dependence and density independence, Acta Theriol., 47, 39–67, https://doi.org/10.1007/BF03192479, 2002.

Szpak, P., Millaire, J. F., White, C. D., and Longstaffe, F. J.: Influence of seabird guano and camelid dung fertilization on the nitrogen isotopic composition of field-grown maize (Zea mays), J. Archaeol. Sci., 39, 3721–3740, https://doi.org/10.1016/j.jas.2012.06.035, 2012.

Żółkoś, K. and Meissner, W.: The effect of grey heron (Ardea cinerea L.) colony on the surrounding vegetation and the biometrical features of three undergrowth species, Pol. J. Ecol., 56, 65–74, 2008.

PAPER VI

Accumulation of chemical elements in yellow-necked mice under a colony of great cormorants.

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Accumulation of chemical elements in yellow-necked mice under a colony of great cormorants

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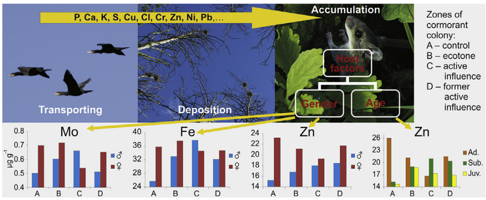
HIGHLIGHTS

- 20 chemical elements in bodies of *Apodemus flavicollis* from a great cormorant colony were studied.
- Concentrations of K, Mn, Cu, Rb, Pb depended on the intensity of cormorant influence.
- Gender-related differences in concentrations of Zn, Fe and Mo were identified.
- Changes in the chemical environment in the cormorant colony affect small mammals.

GRAPHICAL ABSTRACT



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ABSTRACT

This study represents the first investigation into the accumulation of chemical elements in small mammals inhabiting the territory of a great cormorant colony. Trapping was done in the Juodkrantė great cormorant colony, one of the largest colonies in Europe. The accumulation of 20 chemical elements in the bodies (muscle and bones) of yellow-necked mice (*Apodemus flavicollis*) was investigated using the energy-dispersive x-ray fluorescence equipment Spectro Xepos HE. Two groups of positively intercorrelated chemical elements (Mg, Al, P, Ca and Al, S, Cl, K) were identified. The concentrations of five elements differed significantly between mice trapped in different zones of the colony with differing intensities of cormorant influence: the values of K and Cu in *A. flavicollis* increased in line with an increase in the influence of the cormorants, while the concentrations of Rb and Pb decreased. The concentrations of Mn differed between zones, but were not related to the intensity of bird influence. Differences in the concentration of Zn (ANOVA $F = 24.38$; $p < 0.001$), Fe ($F = 4.60$; $p < 0.05$) and Mo ($F = 4.47$; $p < 0.05$) were related to the gender factor, all concentrations being higher in females. The concentrations of Zn were age-dependent, being highest in adult individuals ($21.7 \pm 4.5\ \mu g\ g^{-1}$) and exceeding those in subadult ($19.4 \pm 3.4\ \mu g\ g^{-1}$) individuals or juveniles ($16.7 \pm 1.3\ \mu g\ g^{-1}$). In general, the concentrations of accumulated elements in *A. flavicollis* from the territory of the cormorant colony were lower than in rodents from industrially polluted sites.

1. Introduction

Atmospheric deposition and anthropogenic activities (agriculture, mining, combustion, industry) release significant quantities of trace elements and heavy metals. Entering water ecosystems, these

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substances accumulate in hydrobionts or deposit in bottom sediments (Yi et al., 2011; Gajdoš and Janiga, 2015; Hsu et al., 2016). Great cormorants (*Phalacrocorax carbo sinensis*), like other piscivorous birds breeding in colonies, play an important role in transporting nutrients from water to land ecosystems (Osono et al., 2002; Ellis et al., 2006; Gwiazda et al., 2010; Klimaszyk et al., 2015; Otero et al., 2015). Most trees, shrubs and other plants in the territories of cormorant colonies die after few years due to over-fertilization (Garcia et al., 2011) and are replaced by other plant communities (Ayers et al., 2015; Matulevičiūtė et al., 2018). Lichen and fungal communities also change (Osono et al., 2002), as do communities of insects, spiders and lizards (Polis and Hurd, 1996). Most of these changes are related to N and P levels in the soil, which can be increased by 10^4 to 10^5 times (Garcia et al., 2011). Trace elements, including hazardous heavy metals, enter the soil from cormorant excrements (Taraškevičius et al., 2013). Though some trace elements (Al, Fe, Ni, Cu, Zn, Sr, Mo) are harmful at higher concentrations, macroelements (Na, Mg, K, Ca) may be beneficial (Pais and Jones, 1997; Hernout et al., 2016).

Concentrations of heavy metals and trace elements have recently been investigated in different animal taxa, including insects (Aydogan et al., 2017), crustaceans (Gedik et al., 2017), fish (Yi et al., 2011; Benzer, 2017), amphibians (Qureshi et al., 2015), reptiles (Nasri et al., 2017), birds (Kral et al., 2017) and mammals (Lehel et al., 2015; Neila et al., 2017). Small mammals have been (Wren, 1986) and remain a favourite object for research into metal and trace element accumulation (Martiniaková et al., 2012; Gajdoš and Janiga, 2015; Bortey-Sam et al., 2016; Khazaee et al., 2016). Accumulation of heavy metals in small mammals has been well documented in polluted areas, including near mines (Phelps and McBee, 2009; Bortey-Sam et al., 2016; Khazaee et al., 2016), power stations (Martiniaková et al., 2010) and paper mills (Gajdoš and Janiga, 2015). Small mammals serve as suitable objects to study the accumulation of heavy metals and trace elements, as the concentrations of the metals in the bodies, organs or tissues of the animals reflect the residues in the soil (Shore and Rattner, 2001; Ieradi et al., 2003; Martiniaková et al., 2011 and references therein). As a research subject, yellow-necked mouse (*Apodemus flavicollis*) was chosen for several reasons. In particular, *A. flavicollis* is the most abundant small mammal species in the territory of the investigated great cormorant colony (Balčiauskas et al., 2016). Additionally, it is characterized by intensive metabolism, a granivorous/insectivorous diet and small individual territories (Butet and Delettre, 2011; Gajdoš and Janiga, 2015). The home range median value for *A. flavicollis* has been identified as 625 m^2 for males and 551 m^2 for females (Vukićević-Radić et al., 2006). *A. flavicollis* is also known as proper biomonitor of metal pollution (Petkovšek et al., 2014), with increased levels of metals in the organism relating to environmental pollution (Martiniaková et al., 2011). In our study, we analysed chemical elements in the muscles and bones of the skinned bodies of *A. flavicollis*. In comparison to internal organs, bones accumulate metals over a longer time period (Martiniaková et al., 2011, 2012) and, as very few *A. flavicollis* individuals live longer than a year, it can be considered to reflect the elemental load of the year of trapping (Martiniaková et al., 2010; Gajdoš and Janiga, 2015).

Various aspects of the influence of great cormorant and other colonial bird colonies on the environment are known already (Ayers et al., 2015; Lafferty et al., 2016). However, investigations into the accumulation of heavy metals and trace elements in small mammals inhabiting these colonies are lacking. The investigated colony in Juodkrantė is one of the biggest in Europe, with a maximum number of breeding pairs being 3800 in 2015 (V. Knyva, pers. com). Feeding in both marine and inland waters, including aquaculture, great cormorants are almost purely piscivourous and the estimated biomass of consumed fish in the Juodkrantė colony is ca. 700 tons per year (Pūtys, 2012), with part of this biomass thereafter reaching the ground in the colony in the form of excrement and lost fish, as well as dead chicks during the breeding season.

This study represents the first investigation into heavy metals and trace elements in small mammals occupying the territory of a colony of great cormorants. Research concerning the ecology of mammals in the colonies of great cormorant is still very limited, but decreases in the diversity of the small mammal community and a reduction in abundance have been described in relation to the great cormorant colony in Juodkrantė (Balčiauskienė et al., 2014), along with alterations in the population structure and a decline in body condition (Balčiauskas et al., 2015). Reductions in *A. flavicollis* body weight, body length and index of body condition, as well as changes in skull size and shape, were greatest in the most affected zones of the colony (Balčiauskienė et al., 2015; Balčiauskas et al., 2016). Increased stable isotope signatures in the small mammals, related to the intensity of cormorant influence, show the consequences of biological pollution (Balčiauskas et al., 2016). We hypothesized that such changes may be related to variations in the concentrations of chemical elements in the tissues of the small mammals. To test the hypothesis, we studied the concentrations of 20 elements in the skinned bodies of *A. flavicollis* trapped in different zones with different levels of impact by great cormorants. Differences in accumulation depending on age and gender of mice were evaluated.

2. Material and methods

2.1. Study site

Small mammals were trapped in a colony of great cormorants situated in the western part of Lithuania near Juodkrantė on the Curonian Spit (WGS 55° 31′ 14.22″, 21° 6′ 37.74″). This colony is the largest in Lithuania and one of the largest in Europe. It is also distinguished by high biological pollution reflected even in small mammals, encompassing all investigated aspects of their biology and ecology (Balčiauskas et al., 2015). The number of breeding pairs reached 3800 in 2015 (V. Knyva, pers. com.) and the area of the colony covers around 12 ha. Four zones with differing levels of colony influence have been defined in the territory (Fig. 1):

Zone A – the control zone. This is outside the colony and there is no direct influence by nesting cormorants on the habitat.
Zone B – the zone of the ecotone. This is located between zones C and D and the surrounding forests that are not influenced by the colony. There are few nests in this zone and the influence of the cormorants is weak.
Zone C – the zone of active influence. This is the active part of the colony with the highest concentration of nests and the strongest influence of the colony.
Zone D – the zone of former active influence. Nests are already abandoned and trees are dead, many of them rotten, fallen and decaying.

2.2. Small mammal sampling

Small mammals were trapped in the middle of September 2015, using snap-trap lines, each consisting of 25 traps spaced 5 m from each other. Traps were baited with brown bread soaked in sunflower oil. Exposition of traps was three days (Balčiauskas et al.,

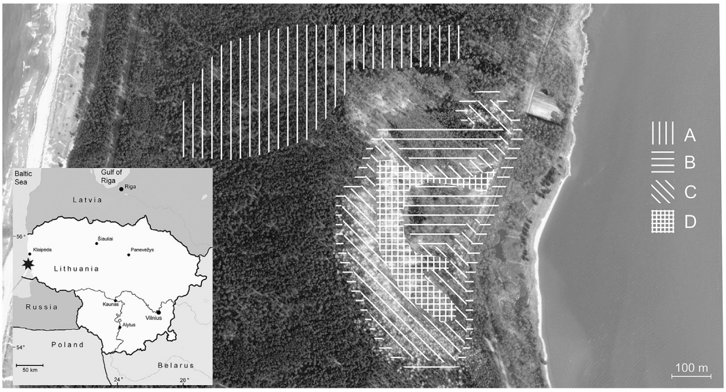

Fig. 1. Investigation site (marked by star at inlay map of Lithuania) and location of the zones in the great cormorant colony in Juodkrantė, 2015. Zone A – control, zone B – ecotone between the colony and surrounding forest, zone C – active influence of the colony, zone D – zone of the former influence.

2016). Trapping effort was 750 trap-days. In total, 132 individuals of six small mammal species were trapped: common shrew (*Sorex araneus*), bank vole (*Myodes glareolus*), field vole (*Microtus agrestis*), root vole (*Microtus oeconomus*), harvest mouse (*Micromys minutus*) and yellow-necked mouse (*Apodemus flavicollis*). The dominant species was *A. flavicollis* (70.5% of all trapped small mammals) and the subdominant *M. glareolus* (22.7%). Other small mammal species were insufficiently represented in the various zones of the colony.

Chemical analysis was conducted on the dominant species, *A. flavicollis*. Migration of individuals between zones was investigated in 2013 using live traps and the capture-mark-recapture method. No migration cases were identified.

Before dissection, individuals were weighed (to an accuracy of 0.1 g) and measured with sliding callipers (accuracy of 0.1 mm). The gender and age of the animals were determined during dissection. We used three age categories, adult (ad.), subadult (sub.) and juvenile (juv.), depending on the presence and involution of the *gl. thymus* (involuted in adults, disappearing in subadults, functioning in juveniles) and reproductive status (Balčiauskas et al., 2015). Samples were placed in separate bags, labelled and stored in a freezer at a temperature below −18 °C.

2.3. *Study of chemical elements*

Chemical elements were analysed in 54 individuals (23 males, 31 females/21 adults, 21 subadults and 12 juveniles) of the dominant species *A. flavicollis*. We used the skinned body (muscle and bones without intestines, hereafter "body") to register the presence and concentration of the following 20 elements: Na, Mg, Al, Si, P, S, Cl, K, Ca, V, Mn, Fe, Ni, Cu, Zn, Br, Rb, Sr, Mo and Pb. The sampling unit used was body of one individual.

Samples were oven dried at 100 °C for 12 h, crushed in agate mortars and later pre-mineralized to dry ash at 240 °C to avoid possible ignition and content loss for some volative elements (Markova and Rustschev, 1994; Koh et al., 1999). Ashed samples were milled using the MM 400 mill with zirconium oxide grinding jars and grinding balls (milling time 6 min, frequency 27 Hz). Milled samples were mixed with the Licowax binder (Fluxana) in the proportions of 1.25 g of material and 0.28 g of binder (dilution factor 0.816, as recommended by the equipment manufacturers). Each sample was homogenised and pressed for 3 min using 15 KN (press PP25) to produce 20 mm diameter pellets (Taraškevičius et al., 2017a). The pellets were analysed by energy-dispersive x-ray fluorescence (EDXRF) equipment Xepos HE (Kleve, Germany) using TurboQuant (TQ) II for pellets calibration module as elaborated by the manufacturers. The TQ method combines different procedures: calculation of the mass attenuation coefficient, using the extended Compton model, and final calibration based on fundamental parameters method.

Samples were re-calibrated using standard bovine muscle (BOVM-1) and the International Plant-Analytical Exchange (IPE) program. Four extra sub-samples were taken from each of the IPE Material Samples and from the BOVM-1. Every fifth milled sample (10 extra sub-samples in total) of *A. flavicollis* was divided into two parts to produce an additional second sub-sample of the same primary material. The average values of the variation coefficients of paired sub-samples (RSD) were: < 5% for Na, Mg, Al, P, S, Cl, K, Ca, Mn, Fe, Cu, Br, Rb and Sr; 5–10% for Ni and Zn; 14% for Mo; and 20–23% for Si, V and Pb. The detection limits (μg g^{-1}) of Na, Mg, Al, Si, P, S, Cl, K, Ca, V, Mn, Fe, Ni, Cu, Zn, Br, Rb, Sr, Mo and Pb were 75, 36, 23, 1.5, 2.2, 0.6, 0.8, 1.2, 0.9, 0.3, 0.2, 0.8, 1.0, 0.5, 0.2, 0.06, 0.06, 0.07, 0.2 and 0.2 respectively. Concentrations of chemical elements were expressed on a wet weight basis in μg g^{-1} (the weight loss on average is 412%).

Preparations were made at the Nature Research Centre (Vilnius) and the analysis of the prepared samples was carried out (Spectro Xepos HE) at the Marine Research Institute, Klaipėda University.

2.4. *Statistical analysis*

In our analysis, we utilized the mean, range (min–max) and standard deviation of concentrations, Pearson's correlation coefficients and their significance. The normality of the distribution of concentrations was evaluated using Kolmogorov-Smirnov's test (13 out of 20 elements conformed to normal distribution). Based on conformity to normal distribution, parametric tests were used. The influences of multifactors were tested using MANOVA. The influences of zone, gender and age were tested using two-way ANOVA with Wilk's lambda for significance. The Tukey post-hoc test was used to compare multiple independent groups. The minimum significance level was set at $p < 0.05$. We used STATISTICA 6.0 for Windows.

3. Results

3.1. Interaction of host and site factors

The concentrations of chemical elements in *A. flavicollis* depended on which zone of the great cormorant colony they inhabited (MANOVA Wilks $\lambda = 0.04$, $F_{3,53} = 2.90$, $p < 0.001$) and the gender of the animals (Wilks $\lambda = 0.41$, $F_{1,53} = 2.06$, $p < 0.05$), but in most cases did not depend on the age of the animals (Wilks $\lambda = 0.29$, $F_{2,53} = 1.20$, $p = 0.262$). However, animal age did have a significant impact on the concentrations of Zn in *A. flavicollis*.

Differences in the concentrations of chemical elements did not depend upon interaction of site-based and host factors: age × site (two-way ANOVA $F = 1.14$, $p = 0.225$) and gender × site ($F = 1.16$, $p = 0.264$). However, the interaction of two host factors, i.e., age × gender, did have a statistically significant influence ($F = 1.93$, $p < 0.05$).

3.2. Influence of the great cormorants: the zone factor

Depending on which zone of the great cormorant colony the mice had been trapped in, concentrations of K (ANOVA $F = 6.45$, $p < 0.001$), Mn ($F = 7.04$, $p < 0.001$), Cu ($F = 3.40$, $p < 0.05$), Rb ($F = 14.59$, $p < 0.001$) and Pb ($F = 5.15$, $p < 0.05$) differed in the individuals of *A. flavicollis* (Table S1). The concentration of K was significantly higher in mice from zone D than in zone A (Tukey HSD, $p < 0.01$) and zone C ($p < 0.01$). The concentration of Mn was at its highest in mice from zones A and C. The concentration of Mn in zone A was significantly higher than in zone B (Tukey HSD, $p < 0.01$) and zone D ($p < 0.001$), and the concentration of Mn in zone C was significantly higher than in zone D (Tukey HSD, $p < 0.05$). The concentration of Cu was at its highest in mice from zone C (significantly higher than in zone A, Tukey HSD, $p < 0.05$), though not significantly differing from zone B ($p = 0.09$) and D ($p = 0.71$) (Table S1).

The concentration of Rb in mice from zone A was higher than in zones B, C and D (Tukey HSD, all $p < 0.001$), while the concentration in zone B was higher than in zone D ($p < 0.05$). Similarly, the concentration of Pb was at its highest in mice from zone A (differences from all other zones significant at $p < 0.05$). Thus, the concentrations of K and Cu in *A flavicollis* increased in line with an increased influence of the cormorants, while the concentrations of Rb and Pb decreased (Table S1, Fig. 2).

3.3. Differences related to the gender and age of the mice: the host factor

Differences in the concentrations of Zn (ANOVA $F = 24.38$; $p < 0.001$), Fe ($F = 4.60$; $p < 0.05$) and Mo ($F = 4.47$; $p < 0.05$) were related to the gender factor, all concentrations being higher in females (Table 1). We also found that, for some elements, zone factor

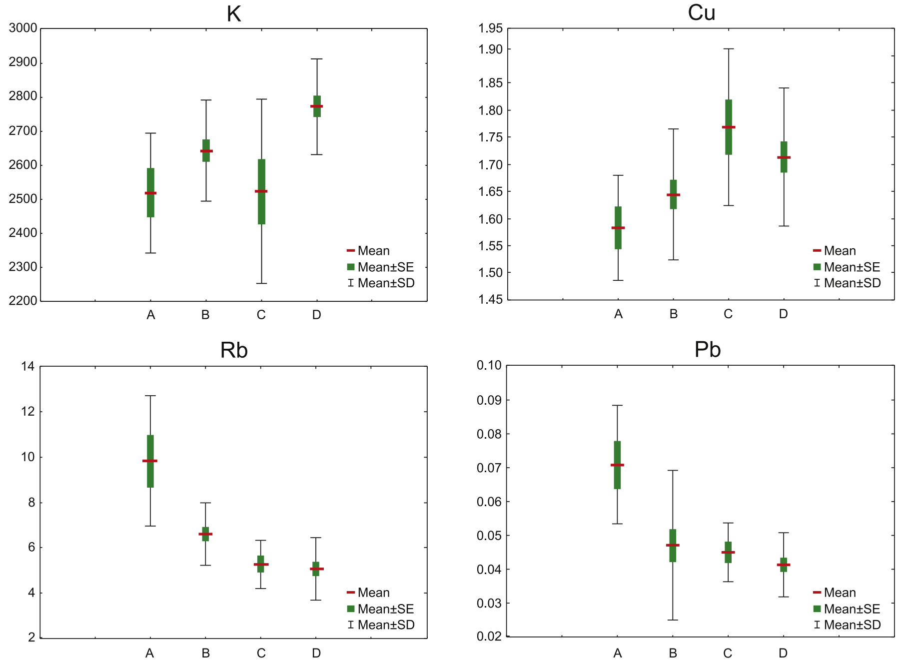

Fig. 2. Concentrations of K, Cu, Rb and Pb ($\mu g\ g^{-1}$) in the bodies of *Apodemus flavicollis* from the different zones of the great cormorant colony (age and gender groups pooled). Zone A – control, zone B – ecotone between colony and surrounding forest, C – zone of active influence of the colony, D – zone of former influence.

Table 1
Concentrations of chemical elements ($\mu g\ g^{-1}$) in the bodies of *Apodemus flavicollis* trapped in various zones of the great cormorant colony, according to age and gender groups. Significant differences between groups is presented in bold (ANOVA: * – $p < 0.05$, ** – $p < 0.001$). Superscript letters indicate pairwise age-group differences.

Element	Adults (N = 21)		Subadults (N = 21)		Juveniles (N = 12)		Females (N = 31)		Males (N = 23)	
	Mean ± SD	Min–Max	Mean ± SD	Min–Max	Mean ± SD	Min–Max	Mean ± SD	Min–Max	Mean ± SD	Min–Max
Na	708 ± 103	437–929	681 ± 86	523–852	688 ± 69	577–826	706 ± 71	558–852	676 ± 108	437–929
Mg	298 ± 43	199–366	276 ± 43	207–367	298 ± 29	255–360	298 ± 39	227–367	277 ± 41	199–366
Al	81.7 ± 9.3	63.9–96.4	79.8 ± 11.4	59.6–103.9	80.5 ± 10.6	69.4–100.5	80.9 ± 10.3	63.2–103.9	80.4 ± 10.5	59.6–100.5
Si	23.6 ± 21.5	1.5–86.1	29.4 ± 36.0	1.5–149.0	29.3 ± 23.7	2.7–70.1	27.0 ± 23.9	1.5–82.0	27.2 ± 33.5	1.5–149.0
P	4952 ± 528	4106–5996	4772 ± 564	3869–6099	4949 ± 322	4420–5469	4971 ± 496	3973–6099	4760 ± 501	3869–5996
S	2438 ± 328	1738–2977	2280 ± 375	1676–3084	2154 ± 300	1683–2551	2327 ± 335	1710–3084	2294 ± 384	1676–3021
Cl	781 ± 83	628–941	763 ± 74	643–932	761 ± 46	693–831	782 ± 70	643–941	752 ± 73	628–894
K	2721 ± 187	2300–3119	2635 ± 184	2184–2961	2591 ± 206	2242–2880	2670 ± 209	2184–3119	2643 ± 174	2300–2944
Ca	7483 ± 1167	5435–9933	6905 ± 1243	5167–9851	6965 ± 630	5879–7899	7364 ± 1071	5167–9851	6845 ± 1139	5207–9933
V	0.16 ± 0.02	0.12–0.22	0.15 ± 0.02	0.11–0.18	0.15 ± 0.02	0.11–0.18	0.16 ± 0.02	0.11–0.22	0.15 ± 0.02	0.11–0.18
Mn	0.78 ± 0.28	0.48–1.50	0.70 ± 0.34	0.42–2.03	0.88 ± 0.39	0.43–1.75	0.82 ± 0.32	0.43–1.75	0.71 ± 0.34	0.42–2.03
Fe*	34.7 ± 4.2	29.9–42.6	33.4 ± 6.9	22.0–54.9	35.9 ± 3.8	30.3–42.7	**35.8 ± 5.5**	**27.9–54.9**	**32.7 ± 4.8**	**22.0–42.1**
Ni	0.62 ± 0.10	0.38–0.82	0.61 ± 0.12	0.43–0.85	0.6 ± 0.12	0.36–0.78	0.61 ± 0.11	0.36–0.85	0.6 ± 0.1	0.43–0.79
Cu	1.66 ± 0.13	1.37–1.86	1.67 ± 0.12	1.47–1.95	1.74 ± 0.16	1.5–2.03	1.69 ± 0.14	1.46–2.03	1.67 ± 0.13	1.37–2.00
Zn**	$\mathbf{21.7 \pm 4.5}^{S,J}$	**15.3–23.2**	$\mathbf{19.4 \pm 3.4}^{A,J}$	**14.5–24.3**	$\mathbf{16.7 \pm 1.3}^{A,S}$	**14.7–18.6**	**21.3 ± 4.3**	**14.7–28.2**	**17.5 ± 2.3**	**14.5–23.5**
Br	2.38 ± 0.48	1.28–3.17	2.35 ± 0.57	0.88–3.59	2.65 ± 0.37	1.99–3.23	2.41 ± 0.56	0.88–3.59	2.45 ± 0.41	1.58–3.11
Rb	6.27 ± 2.45	3.43–13.49	6.16 ± 2.25	3.76–12.23	6.18 ± 1.15	4.74–8.28	6.35 ± 2.26	3.76–13.49	6 ± 1.93	3.43–12.23
Sr	3.14 ± 1.26	1.91–8.03	2.78 ± 0.51	2.15–4.47	2.60 ± 0.36	2.11–3.28	3.03 ± 1.07	2.08–8.03	2.69 ± 0.49	1.91–3.89
Mo*	0.66 ± 0.19	0.32–1.09	0.61 ± 0.17	0.27–0.88	0.57 ± 0.19	0.24–0.88	**0.66 ± 0.18**	**0.32–1.09**	**0.56 ± 0.16**	**0.24–0.88**
Pb	0.05 ± 0.02	0.02–0.12	0.05 ± 0.02	0.02–0.08	0.04 ± 0.01	0.02–0.05	0.05 ± 0.02	0.02–0.12	0.04 ± 0.01	0.02–0.08

had a differing influence on males and females. In females, the concentrations of K (ANOVA, $F = 4.35$, $p < 0.05$) and Cu ($F = 3.12$, $p < 0.05$) differed according to the zone of colony, while this concentration did not differ in males ($F = 1.69$, $p = 0.20$ and $F = 0.73$, $p = 0.16$, respectively). Vice versa, the concentrations of Fe significantly differed according to the zone of the colony in males ($F = 3.57$, $p < 0.05$), but not in females ($F = 0.58$. $p = 0.64$).

Age-related differences were found in the concentrations of Zn ($F = 10.99$, $p < 0.001$). Zn values ($21.7 \pm 4.5\ \mu g\ g^{-1}$) were highest in the bodies of adult individuals, exceeding those in subadult individuals (Tukey HSD, $p < 0.05$) and juveniles ($p < 0.001$), while values in subadults also exceeded juveniles ($p < 0.05$) (Table 1).

3.4. Inter-elemental correlations

Two groups of chemical elements that positively and significantly correlated between each other within the group were identified in the *A. flavicollis* trapped in the territory of the colony of great cormorants - the first group comprised Mg, Al, P and Ca, while the second group was Al, S, Cl and K (excluding K-Cl, $r = 0.252$, $p = 0.066$) (Fig. 3). Outside these groups, strong significant positive correlations in the concentrations were also found between the pairs Br-Fe ($r = 0.555$, $p < 0.001$) and Sr-Pb ($r = 0.568$, $p < 0.001$).

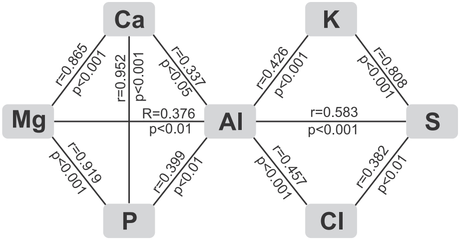

Fig. 3. Intercorrelations between the concentrations of chemical elements in *Apodemus flavicollis* trapped in the territory of the colony of great cormorants (animals from all zones pooled). The correlation between K and Cl ($r = 0.252$, $p = 0.066$) is not shown.

Other correlations between the concentrations of chemical elements are presented in Table S2.

4. Discussion

Cormorants mediate the transfer of various chemical elements from aquatic to terrestrial ecosystems. The main source of this transfer is bird excreta (Klimaszyk et al., 2015; Otero et al., 2015). Pedogeochemical analysis has shown that guano has a low pH, high levels of P, K and Ca (Breuning-Madsen et al., 2010; Lafferty et al., 2016) and raised concentrations of S, Cl, Cr, Ni, Cu, Zn and Pb (Taraškevičius et al., 2013). As was emphasized by the latter author, "geochemical disbalance can be one of the possible reasons of disturbance in natural ecosystems". The other possible source of cormorant-borne chemical elements are the fish brought to the colony as food for chicks, some of these being lost and thus reaching the ground (Pūtys, 2012). In fish from water bodies in Lithuania, the accumulation of heavy metals follows the order Cd > Pb > Ni > Zn > Cr > Cu (Idzelis et al., 2008), with concentrations of Cd and Pb frequently exceeding the Maximum Tolerable Limit value of both Lithuania and the European Union (Staniskiene et al., 2006).

In general, the accumulation of trace elements and heavy metals in mammals depends on habitat, available food, season and host factors, such as species, age and gender (Fritsch et al., 2010; Lehel et al., 2015; Neila et al., 2017). Although almost any chemical elements can be detrimental to organisms at high doses, some of these elements (Na, Mg, K, Ca) are not only essential at lower concentrations, but are also frequently lacking in organisms. Amongst these, essential elements such as Al, Fe, Ni, Cu, Zn, Sr and Mo can be toxic in high concentrations, while Pb and Cd may be toxic even at low concentrations (Pais and Jones, 1997; Hernout et al., 2016).

Our study was the first investigation into the accumulation of chemical elements in small mammals inhabiting the territories of great cormorant colonies. The main factor determining the concentrations of the chemical elements in *A. flavicollis* was the zone of the colony, this characterizing nest density and bird presence, thus a proxy of bird influence on the local environment. We found a significant increase in the concentrations of K and Cu and a decrease in Rb and Pb in *A. flavicollis* trapped in the zones with increased levels of cormorant impact (Table S1). The overall impact of the influence of cormorants can be considered ambiguous in terms of advantageous or disadvantageous – the increase in the essential K and Cu is positive, as is the decrease in the harmful Pb, but the decrease in the essential Rb is negative. A lack of K can be compensated by heightened Rb intake, extending across all the food web (Nyholm and Tyler, 2000), but a deficiency of Rb is reported as harmful (Gajdoš and Janiga, 2015). In fish at least, however, excess Rb in combination with heightened Pb, Mo and As may act as a spermatogenesis inhibitor (Yamaguchi et al., 2007).

Concentrations of some trace elements and heavy metals in the bodies of *A. flavicollis* were gender dependent: females accumulated significantly higher concentrations of Zn, Fe and Mo. As for the higher concentration of Mo in females, our results confirm those of Gajdoš and Janiga (2015). Higher concentrations of Zn have also been found in female rats (Bortey-Sam et al., 2016), as well as human females (Ziola-Frankowska et al., 2015; Taraškevičius et al., 2017b). Research by Zarrintab and Mirzaei (2017) showed opposite results, there a significantly higher level of Zn was found in male rats. Out of all the analysed elements, only the Zn concentration in *A. flavicollis* was age-dependent in the investigated great cormorant colony. The concentration of Zn increased with age, being highest in adult mice. As well as Zn being involved in the development of sex organs, it is necessary for normal growth and maturation. Additionally, juveniles and pregnant or lactating females have increased requirements for zinc (Roohani et al., 2013). However, it is known that the Zn concentration in mammals is regulated at constant concentrations and is mostly present within a narrow range (Hernout et al., 2016). From this point of view, our finding of age dependent Zn concentrations in mice from within the cormorant colony requires further attention. Decreased body size of *M glareolus* and common vole (*Microtus arvalis*) have been observed in Pb, Fe, Cu and Zn contaminated areas of Slovakia (Martiniaková et al., 2011), while similar changes in body size and body condition of black-striped mice (*Apodemus agrarius*), wood mice (*A. sylvaticus*) and greater white-toothed shrews (*Crocidura russula*) have been observed in other polluted areas (Sánchez-Chardi et al., 2007a, 2007b; Velickovic, 2007). A decrease in body mass in *A. flavicollis* in the expanding part of the colony typified by fresh nests was also observed in the investigated colony (Balčiauskas et al., 2015). Comparing heavy metal concentrations in *M. glareolus* from the western part of Lithuania (Mažeikytė and Balčiauskas, 2003), the average concentrations of Pb (0.34 $\mu g\, g^{-1}$) and Cu (2.61 $\mu g\, g^{-1}$) in the bodies of these voles were higher than those accumulated in *A. flavicollis* from the great cormorant colony, while the concentration of Ni (0.61 $\mu g\, g^{-1}$) did not differ (Table S1). However, these concentrations are not directly comparable, as *M. glareolus* is known to accumulate Cd, Pb, Cu and Zn in higher concentrations than *A. flavicollis* (Martiniaková et al., 2010, 2011). In addition, we have no data on the possible transfer of heavy metals and other elements with dust, which may have a significant influence on concentrations in small mammals (Metcheva et al., 2001).

Compared to other rodents from industrially polluted sites, the concentrations of the accumulated elements in *A. flavicollis* from the territory of the cormorant colony were lower. However, the results are very inconsistent (Table S3). It is known that the accumulation of heavy metals may differ by up to fivefold between species of shrews, voles and mice in the same territory (Wijnhoven et al., 2007). We do not discuss these differences with respect to the species, site or organs, but it is clear that biological pollution by cormorants is lower than that by industrial outputs. Still however, we found differences in some element accumulations that did depend on the level of the impact of the cormorant colony (Table S1). Concentrations of Pb in *A. flavicollis* from the territory of the great cormorant colony were lower not only than those in rodents from industrially polluted sites, but also in comparison to concentrations of various chemical elements in the tissues of the cormorants (Goutner et al., 2011; Misztal-Szkudlinska et al., 2011). We found two groups of chemical elements in the bodies of *A. flavicollis* with concentrations correlated within the group, namely Mg, Al, P and Ca, plus Al, S, Cl and K (Fig. 3). Interactions between chemical elements can be related to the specific mineral structure of the bone tissue and physiological functions of these elements in the organism (Brodziak-Dopierala et al., 2009). Strong correlations between Mg, P and Ca have been found in human bones (Ziola-Frankowska et al., 2015), while Gajdoš and Janiga (2015) found strong correlations between S and K. Likewise in our case, the correlation between S and K was very strong ($R = 0.808$, $p < 0.001$). Moreover, we complement this group with correlations with Cl and Al.

We may conclude that the accumulation of five out of 20 investigated elements in the bodies of *A. flavicollis* inhabiting the territory of the great cormorant colony depended on the intensity of bird influence. However, as identified by previous research, this is hardly likely to be the sole reason for significant changes in small mammals (Balčiauskienė et al., 2014, 2015; Balčiauskas et al., 2015, 2016). Many ecological factors are changed due to the biological pollution of the cormorant colony, including the food base for the small mammals, the composition of vegetation, the presence of refuges and disturbance by birds. Chemical changes in the colony resulting from the transfer of materials from the aquatic to terrestrial ecosystem work in complex with these other changes.

The main limitation of our work is the sample size. However, the number of small mammals inhabiting the colony is finite and can hardly be bigger. Investigations into other cormorant colonies and other small mammals, such as bank voles (*Myodes glareolus*), will expand the results of this pilot study and may help to gain a deeper understanding of the registered chemical changes.

Conflicts of interest

The authors have no conflicts of interest to declare.

Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.chemosphere.2018.09.025.

References

Aydogan, Z., Şişman, T., İncekara, U., Gürol, A., 2017. Heavy metal accumulation in some aquatic insects (Coleoptera: Hydrophilidae) and tissues of Chondrostoma regium (Heckel, 1843) relevant to their concentration in water and sediments from Karasu River, Erzurum, Turkey. Environ. Sci. Pollut. Res. 24 (10), 9566–9574.

Ayers, C.R., Hanson-Dorr, K.C., O'Dell, S., Lovel, C.D., Jones, M.L., 2015. Impacts of colonial waterbirds on vegetation and potential restoration of island habitats. Restor. Ecol. 23 (3), 252–260.

Balčiauskas, L., Balčiauskienė, L., Jasiulionis, M., 2015. Mammals under a colony of great cormorants: population structure and body condition of yellow-necked mice. Turk. J. Zool. 39 (5), 941–948.

Balčiauskas, L., Skipitytė, R., Jasiulionis, M., Trakimas, G., Balčiauskienė, L., Remeikis, V., 2016. The impact of Great Cormorants on biogenic pollution of land ecosystems: stable isotope signatures in small mammals. Sci. Total Environ. 565, 376–383.

Balčiauskienė, L., Jasiulionis, M., Balčiauskas, L., 2014. Loss of diversity in a small mammal community in a habitat influenced by a colony of great cormorants. Acta Zool. Bulg. 66 (2), 229–234.

Balčiauskienė, L., Balčiauskas, L., Jasiulionis, M., 2015. Skull variability of mice and voles inhabiting the territory of a great cormorant colony. Biologia 70 (10), 1406–1414.

Benzer, S., 2017. Concentrations of arsenic and boron in water, sediment and the tissues of fish in emet stream (Turkey). Bull. Environ. Contam. Toxicol. 98 (6), 805–810.

Bortey-Sam, N., Nakayama, S.M.M., Ikenaka, Y., Akoto, O., Baidoo, E., Mizukawa, H., Ishizuka, M., 2016. Heavy metals and metalloid accumulation in livers and kidneys of wild rats around gold-mining communities in Tarkwa, Ghana. J. Environ. Chem. Ecotoxicol. 8 (7), 58–68.

Breuning-Madsen, H., Ehlers-Koch, C., Gregersen, J., Lojtnant, Ch.L., 2010. Influence of perennial colonies of piscivorous birds on soil nutrient contents in a temperate humid climate. Geogr. Tidsskr. 110 (1), 25–35.

Brodziak-Dopierala, B., Kwapulinski, J., Kusz, D., Gajda, Z., Sobczyk, K., 2009. Interactions between concentrations of chemical elements in human femoral heads. Arch. Environ. Contam. Toxicol. 57 (1), 203–210.

Butet, A., Delettre, Y.R., 2011. Diet differentiation between European arvicoline and murine rodents. Acta Theriol. 56 (4), 297–304.

Ellis, J.C., Farina, J.M., Witman, J.D., 2006. Nutrient transfer from sea to land: the case of gulls and cormorants in the Gulf of Maine. J. Anim. Ecol. 75, 565–574.

Fritsch, C., Cosson, R.P., Coeurdassier, M., Raoul, F., Giraudoux, P., Crini, N., Vaufleury, A., Scheifler, R., 2010. Responses of wild small mammals to a pollution gradient: host factors influence metal and metallothionein levels. Environ. Pollut. 158 (3), 827–840.

Gajdoš, M., Janiga, M., 2015. Contamination of *Apodemus flavicolis* in the experimental study area – Ružumberok. Oecol. Montana 24, 60–69.

Garcia, L.V., Ramo, C., Aponte, C., Moreno, A., Dominguez, M.T., Gomez-Aparicio, L., Redondo, R., Maranon, T., 2011. Protected wading bird species threaten relict centenarian cork oaks in a Mediterranean biosphere reserve: a conservation management conflict. Biol. Conserv. 144 (2), 764–771.

Gedik, K., Kongchum, M., DeLaune, R., Sonnier, J.J., 2017. Distribution of arsenic and other metals in crayfish tissues (*Procambarus clarkii*) under different production practices. Sci. Total Environ. 574, 322–331.

Goutner, V., Becker, P.H., Liordos, V., 2011. Organochlorines and mercury in livers of great cormorants (*Phalacrocorax carbo sinensis*) wintering in northeastern Mediterranean wetlands in relation to area, bird age, and gender. Sci. Total Environ. 409 (4), 710–718.

Gwiazda, R., Jarocha, K., Szrek-Gwiazda, E., 2010. Impact of a small cormorant (*Phalacrocorax carbo sinensis*) roost on nutrients and phytoplankton assemblages in the littoral regions of a submontane reservoir. Biologia 65 (4), 742–748.

Hernout, B.V., Arnold, K.E., McClean, C.J., Walls, M., Baxter, M., Boxall, A.B., 2016. A national level assessment of metal contamination in bats. Environ. Pollut. 214, 847–858.

Hsu, L.C., Huang, C.Y., Chuang, Y.H., Chen, Y.T., Teah, H.Y., Chen, T.Y., Chang, C.F., Liu, Y.T., Tzou, Y.M., 2016. Accumulation of heavy metals and trace elements in fluvial sediments received effluents from traditional and semiconductor industries. Sci. Rep. 34250 (6), 1–12.

Idzelis, R.L., Kesminas, V., Svecevičius, G., Misius, V., 2008. Accumulation of heavy metals (Cu, Zn, Ni, Cr, Pb, Cd) in tissues of perch (*Perca fluviatilis* L.) and roach *Rutilus rutilus* (L.) under experimental conditions. J. Environ. Eng. Landsc. 16 (4), 205–212.

Ieradi, L.A., Zima, J., Allegra, F., Kotlanova, E., Campanella, L., Grossi, R., Cristaldi, M., 2003. Evaluation of genotoxic damage in wild rodens from a polluted area in the Czech Republic. Folia Zool. 52 (1), 57–66.

Khazaee, M., Hamidian, A.H., Shabani, A.A., Ashrafi, S., Mirjalili, S.A.A., Esmaeilzadeh, E., 2016. Accumulation of heavy metals and as in liver, hair, femur, and lung of Persian jird (*Meriones persicus*) in Darreh Zereshk copper mine, Iran. Environ. Sci. Pollut. Res. 23 (4), 3860–3870.

Klimaszyk, P., Piotrowicz, R., Rzymski, P., 2015. Changes in physico-chemical conditions and macrophyte abundance in a shallow soft-water lake mediated by a Great Cormorant roosting colony. J. Limnol. 74 (1), 114–122.

Koh, S., Aoki, T., Katayama, Y., Takada, J., 1999. Losses of elements in plant samples under the dry ashing process. J. Radioanal. Nucl. Chem. 239 (3), 591–594.

Kral, T., Blahova, J., Doubkova, V., Farkova, D., Vecerek, V., Svobodova, Z., 2017. Accumulation of mercury in the tissues of the great cormorant (*Phalacrocorax carbo*) from common carp. Bull. Environ. Contam. Toxicol. 98 (2), 167–171.

Lafferty, D.J.R., Hanson-Dorr, K.C., Prisock, A.M., Dorr, B.S., 2016. Biotic and abiotic impacts of Double-crested cormorant breeding colonies on forested islands in the southeastern United States. For. Ecol. Manag. 369, 10–19.

Lehel, J., Laczay, P., Gyurcsó, A., Jánoska, F., Majoros, S., Lányi, K., Marosán, M., 2015. Toxic heavy metals in the muscle of roe deer (*Capreolus capreolus*)—food toxicological significance. Environ. Sci. Pollut. Res. 23 (5), 4465–4472.

Markova, K.I., Rustschev, D., 1994. The application of thermal analysis to the study of ignition processes of solid fuels. Thermochim. Acta 234, 85–94.

Martiniaková, M., Omelka, R., Grosskopf, B., Jančová, A., 2010. Yellow-necked mice (*Apodemus flavicollis*) and bank voles (*Myodes glareolus*) as zoomonitors of environmental contamination at a polluted area in Slovakia. Acta Vet. Scand. 52, 58.

Martiniaková, M., Omelka, R., Jančová, A., Stawarz, R., Formicki, G., 2011. Concentrations of selected heavy metals in bones and femoral bone structure of bank (*Myodes glareolus*) and common (*Microtus arvalis*) voles from different polluted biotopes in Slovakia. Arch. Environ. Contam. Toxicol. 60 (3), 524–532.

Martiniaková, M., Omelka, R., Stawarz, R., Formicki, G., 2012. Accumulation of lead cadmium, zinc in bones of small mammals from polluted areas in Slovakia. Pol. J. Environ. Stud. 21 (1), 153–158.

Matulevičiūtė, D., Motiejūnaitė, J., Uogintas, D., Taraškevičius, R., Dagys, M., Rašomavičius, V., 2018. Decline of a protected coastal pine forest under impact of a colony of great cormorants and the rate of vegetation change under ornithogenic influence. Silva Fenn. 52 (2) article id 7699.

Mažeikytė, R., Balčiauskas, L., 2003. Heavy metal concentrations in bank voles (*Clethrionomys glareolus*) from protected and agricultural territories of Lithuania. Acta Zool. Litu. 13 (l), 48–60.

Metcheva, R., Teodorova, S., Topashka-Ancheva, M., 2001. A comparative analysis of the heavy metals and toxic elements loading indicated by small mammals in different Bulgarian regions. Acta Zool. Bulg. 53, 61–80.

Misztal-Szkudlinska, M., Szefer, P., Konieczka, P., Namiesnik, J., 2011. Biomagnification of mercury in trophic relation of great cormorant (*Phalacrocorax carbo*) and fish in the Vistula Lagoon, Poland. Environ. Monit. Assess. 176, 439–449.

Nasri, I., Hammouda, A., Hamza, F., Zrig, A., Selmi, S., 2017. Heavy metal accumulation in lizards living near a phosphate treatment plant: possible transfer of contaminants from aquatic to terrestrial food webs. Environ. Sci. Pollut. Res. 24 (13), 12009–12014.

Neila, C., Hernández-Moreno, D., Fidalgo, L.E., López-Beceiro, A., Soler, F., Pérez-López, M., 2017. Does gender influence the levels of heavy metals in liver of wild boar? Ecotoxicol. Environ. Saf. 140, 24–29.

Nyholm, N.E.I., Tyler, G., 2000. Rubidium content of plants, fungi and animals closely reflects potassium and acidity conditions of forest soils. For. Ecol. Manag. 134 (1), 89–96.

Osono, T., Hobara, S., Fujiwara, S., Koba, K., Kameda, K., 2002. Abundance, diversity, and species composition of fungal communities in a temperate forest affected by excreta of the Great Cormorant *Phalacrocorax carbo*. Soil Biol. Biochem. 34, 1537–1547.

Otero, X.L., Tejada, O., Martin-Pastor, M., Pena, S., Ferreira, T.O., Perez-Alberti, A., 2015. Phosphorus in seagull colonies and the effect on the habitats. The case of yellow-legged gulls (*Larus michahellis*) in the Atlantic Islands National Park (Galicia-NW Spain). Sci. Total Environ. 532, 383–397.

Pais, I., Jones, J.B., 1997. The Handbook of Trace Elements. CRC Press, pp. 1–240.

Petkovšek, S.A.S., Kopušar, N., Kryštufek, B., 2014. Small mammals as biomonitors of metal pollution: a case study in Slovenia. Environ. Monit. Assess. 186 (7), 4261–4274.

Phelps, K.L., McBee, K., 2009. Ecological characteristics of small mammal communities at a superfund site. Am. Midl. Nat. 161, 57–68.

Polis, G.A., Hurd, S.D., 1996. Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. Am. Nat. 147, 396–423.

Pūtys, Ž., 2012. Great Cormorant *Phalacrocorax carbo Sinensis* Diet and its Effect on Fish Community in the Eutrophic Curonian Lagoon Ecosystem. Summary of doctoral dissertation. VUL, Vilnius, pp. 1–48.

Qureshi, I.Z., Kashir, Z., Hashmi, M.Z., Su, X., Malik, R.N., Ullah, K., Hu, K., Dawood, M., 2015. Assessment of heavy metals and metalloids in tissues of two frog species *Rana tigrina* and *Euphlyctis cyanophlyctis* from industrial city Sialkot, Pakistan. Environ. Sci. Pollut. Res. 22 (18), 14157–14168.

Roohani, N., Hurrell, R., Kelishadi, R., Schulin, R., 2013. Zinc and its importance for human health: an integrative review. J. Res. Med. Sci. 18 (2), 144–157.

Sánchez-Chardi, A., Marques, C.C., Nadal, J., da Luz Mathias, M., 2007a. Metal bioaccumulation in the greater white-toothed shrew, *Crocidura russula*, inhabiting an abandoned pyrite mine site. Chemosphere 67 (1), 121–130.

Sánchez-Chardi, A., Peñarroja-Matutano, C., Ribeiro, C.A.O., Nadal, J., 2007b. Bioaccumulation of metals and effects of a landfill in small mammals. Part II. The wood mouse, *Apodemus sylvaticus*. Chemosphere 70 (1), 101–109.

Shore, R.F., Rattner, B.A., 2001. Ecotoxicology of Wild Mammals. Wiley, London.

Staniskiene, B., Matusevicius, P., Budreckiene, R., Skibniewska, K.A., 2006. Distribution of heavy metals in tissues of freshwater fish in Lithuania. Pol. J. Environ. Stud. 15 (4), 585–591.

Taraškevičius, R., Motiejūnaitė, J., Zinkutė, R., 2013. Pedogeochemical anomalies in surroundings of great cormorant colony (case study in Lithuania). E3S Web of Conferences 1.

Taraškevičius, R., Motiejūnaitė, J., Zinkutė, R., Eigminienė, A., Gedminienė, L., Stankevičius, Ž., 2017a. Similarities and differences in geochemical distribution patterns in epiphytic lichens and topsoils from kindergarten grounds in Vilnius. J. Geochem. Explor. 183, 152–165.

Taraškevičius, R., Zinkutė, R., Gedminienė, L., Stankevičius, Ž., 2017b. Hair geochemical composition of children from Vilnius kindergartens as an indicator of environmental conditions. Environ. Geochem. Health. https://doi.org/10.1007/s10653-017-9977-7.

Velickovic, M., 2007. Measures of the developmental stability, body size and body condition in the black-striped mouse (*Apodemus agrarius*) as indicators of a disturbed environment in northern Serbia. Belg. J. Zool. 137 (2), 147–156.

Vukićević-Radić, O., Matić, R., Kataranovski, D., Stamenković, S., 2006. Spatial organization and home range of *Apodemus flavicollis* and *A. agrarius* on mt. Avala, Serbia. Acta Zool. Acad. Sci. Hungar. 52 (1), 81–96.

Wijnhoven, S., Leuven, R.S.E.W., Velde, G., Jungheim, G., Koelemij, E.I., Vries, F.T., Eijsackers, H.J.P., Smits, A.J.M., 2007. Heavy-metal concentrations in small mammals from a diffusely polluted floodplain: importance of species- and location-specific characteristics. Arch. Environ. Contam. Toxicol. 52, 603–613.

Wren, C.D., 1986. Mammals as biological monitors of environmental metal levels. Environ. Monit. Assess. 6 (2), 127–144.

Yamaguchi, S., Miura, C., Ito, A., Agusa, T., Iwata, H., Tanabe, S., Miura, T., 2007. Effects of lead, molybdenum, rubidium, arsenic and organochlorines on spermatogenesis in fish: monitoring at Mekong Delta area and in vitro experiment. Aquat. Toxicol. 83 (1), 43–51.

Yi, Y., Yang, Z., Zhang, S., 2011. Ecological risk assessment of heavy metals in sediment and human health risk assessment of heavy metals in fishes in the middle and lower reaches of the Yangtze River basin. Environ. Pollut. 159 (10), 2575–2585.

Zarrintab, M., Mirzaei, R., 2017. Evaluation of some factors influencing on variability in bioaccumulation of heavy metals in rodents species: *Rombomys opimus* and *Rattus norvegicus* from central Iran. Chemosphere 169, 194–203.

Ziola-Frankowska, A., Kubaszewski, A., Dabrowski, M., Kowalski, A., Rogala, P., Strzyzewski, W., Labedz, W., Uklejewski, R., Novotny, K., Kanicky, V., Frankowski, M., 2015. The content of the 14 metals in cancellous and cortical bone of the hip joint affected by osteoarthritis. BioMed Res. Int. 2015, 1–23.

PAPER VII

Resource partitioning confirmed by isotopic signatures allows small mammals to share seasonally flooded meadows

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ORIGINAL RESEARCH

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Resource partitioning confirmed by isotopic signatures allows small mammals to share seasonally flooded meadows

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Abstract

Meadows in river deltas are characterized by a high diversity and abundance of small mammals. However, neither their spatial arrangement nor differences in their use of microhabitat can necessarily explain the dense co-occurrence of sympatric species. We investigated how several small mammal species share a seasonally flooded meadow of limited size, testing predictions (P1) that herbivore, granivore, insectivore, and omnivore species are separated in time (dominant in different years), (P2) that sympatric species undergo isotopic partitioning, and (P3) that there are intraspecific differences in diet. Stable carbon and nitrogen isotope signatures in the hair of seven synantropic shrew, vole, and mice species were used as a proxy for their diet. We found that the three most abundant species in eight of the nine years were from different diet groups. However, based on the number of species in the functional groups, the state of small mammal community was considered unfavored in five out of the nine investigation years. In years with the greatest dominance of *Apodemus agrarius*, the small mammal community was characterized by decreased diversity and *Micromys minutus* was either in low abundance or absent. In 2014 and 2016, years of low abundance or absence of *M. oeconomus*, *M. agrestis*, and *M. glareolus* were both recorded in high numbers. Differences in the isotopic signatures of the three most abundant small mammal species in the community were clearly expressed and core areas in the isotopic space were separated, showing their dependence on different dietary resources. Intraspecific dietary separation between young and adult animals was observed only in *M. oeconomus*. Thus, the high species diversity of small mammals and the formation of their community in this investigated flooded meadow are maintained by isotopic partitioning (segregation in dietary space) and by changes in their number over time (shifting dominance).

KEYWORDS
dietary separation, diversity, isotopic partitioning, small mammal community, spring floods

1 | INTRODUCTION

Co-occurring species inevitably will compete for space and resources, and this competition changes their distribution (Baltensperger, Huettmann, Hagelin, & Welker, 2015). While dense co-occurrence of sympatric species may be attributed to differences in microhabitat use (Jorgensen, 2004), not all cases can be explained by this "microhabitat paradigm" (Balestrieri et al., 2017). Alternative means to coexist can be through a spatial arrangement of species (Myllymäki, 1977; Wilson et al., 2014), differing diets (Shiels et al., 2013), or via dietary separation of species with similar requirements, that is, resource partitioning (Calandra et al., 2015; Dueser & Shuggart, 1979; Meserve, 1981; Schoener, 1974; Symes, Wilson, Woodborne, Shaikh, & Scantlebury, 2013). Additional drivers may also influence the temporal and spatial placement of resources and small mammals (Balestrieri et al., 2017; Marques, Rocha, Mendes, Fonseca, & Ferreira, 2015; Sozio & Mortelliti, 2016).

River floodplains, affected by periodic floods, are productive and heterogeneous habitats (Mathar, Kleinebecker, & Hölzel, 2015), suitable for small mammals (Wijnhoven, Smits, Van der Velde, & Leuven, 2006). After recovery from the detrimental influences of floods, the abundance of small mammals in river floodplains is high for a given period of time (Golet, Hunt, & Koenig, 2013).

Areas subject to periodic flooding maintain a high small mammal diversity (Balčiauskas, Balčiauskienė, & Janonytė, 2012b; Crnobrnja-Isailović et al., 2015) as the dynamic hydrology supports a diversity of resources (Merwe & Hellgren, 2016). A greater number of species (Barnosky, Hadly, Maurer, & Christie, 2001; Hallett, 1991) or functional diversity of these species (Wood, McKinney, & Loftin, 2017) enhances the stability of a community, increasing the potential to withstand negative influences (Scheffer et al., 2012). Under conditions of increased and more frequent floods (prognosis by Reader, Stedmon, & Kritzberg, 2014), ecosystems may reorganize (Brown, Whitham, Ernest, & Gehring, 2001). The arrival of new species and resulting changes in food webs (Baltensperger et al., 2015) may be buffered by compensation from complementary species.

Rodent species are characterized by different diets, and thus, the isotopic niche of this complex taxonomic group is broad (Galetti, Rodarte, Neves, Moreira, & Costa-Pereira, 2016). The diets of voles and mice partially overlap, but fundamentally differ from other small mammals such as marsupials and shrews (Baltensperger et al., 2015; Butet & Delettre, 2011; Galetti et al., 2016; Symes et al., 2013). In small rodent communities from transitional temperate climates, three groups are recognized according to their diet, specifically herbivorous voles (*Microtus* and *Arvicola*), granivorous mice (*Apodemus* and *Micromys*), and the omnivorous *M. glareolus* (Butet & Delettre, 2011; Zub, Jędrzejewska, Jędrzejewski, & Bartoń, 2012). All shrews (*Sorex* and *Neomys*) in the temperate region are insectivorous, with the species utilizing dietary separation and microhabitat selection to allow them to coexist in the same habitat (Churchfield & Rychlik, 2006; Pernetta, 1976).

Diet differences may favor coexistence in sympatric species (Kronfeld-Schor & Dayan, 1999; Luo & Fox, 1996; Shiels et al., 2013) and are also characteristic of other systematic groups of mammals, for example, carnivores (Kasper, Peters, Christoff, & de Freitas, 2016).

Small mammal communities are not randomly assembled, they follow so-called "assembly rule" (Fox & Kirkland, 1992). It says that "each species entering a community will tend to be drawn from a different group until each group is represented, and then the rule repeats" (Fox & Brown, 1993). According to Fox (1987), we should expect a single species from each of the different dietary groups to form the community in years with low small mammal diversity, with increasing resources thereafter allowing the addition of a second species from each group, then a third, ultimately resulting in a favorable community structure (see Data analysis). As these small mammal groups reflect dietary separation, isotopic partitioning also should be expected (Calandra et al., 2015; Hwang, Millar, & Longstaffe, 2007).

The aim of the study was to investigate the pattern of coexistence of several small mammal species in a seasonally flooded meadow, based on the working hypothesis that, in order to coexist in a small area, species should be separated not only in dietary space but also in time. We supposed that separation in dietary space would operate for a single year, while shifting dominance would operate over the longer periods, this additionally reflecting the differing resilience of various species to floods. We tested three predictions: P1—sympatric species of the same group (herbivores, granivores, insectivores, and omnivores) are separated by time, that is, dominate in different years, P2—sympatric species are separated in dietary space, thus differ in isotopic signatures, and P3—intraspecific differences between various demographic groups are present (assuming intraspecific competition for food). P3 is based on our previous and ongoing research (Balčiauskas, Skipitytė, Jasiulionis, Balčiauskienė, & Remeikis, 2018; Balčiauskas et al., 2016), where we found some intraspecific segregation in the isotopic space in yellow-necked mice (*Apodemus flavicollis*) and bank voles (*Myodes glareolus*) living in great cormorant colonies, an environment where foods are scarce, thus necessitating competition.

2 | MATERIAL AND METHODS

2.1 | STUDY SITE

We studied the small mammal community of a flooded meadow (55°19′26.23″N, 21°20′24.15″E) near Rusnė settlement (55°20′10′′N; 21°18′54′′E) in the Nemunas River Delta, situated in western Lithuania (Figure 1). The delta is on the border of two major biogeographical regions in Europe (European Environment Agency, 2002), namely the boreal and continental, and thus, the small mammal community encompasses species from both.

The area of the site is quite small (7.05 ha, with a perimeter of 1,070 m) and is flooded every year (Balčiauskas et al., 2012b), with the duration of submergence dependent on flood height. Regardless of flood level, the trapping site is totally flooded for only a short time each spring. Spring floods normally start around 19 of March, and the average duration of flood is 16 days (Floods, 2018). In the study area, spring floods effectively eradicate the small mammal communities in the meadow, but the negative effects are short-term and high small mammal diversities are restored during the summer period from enclosing levees, serving as refugees during flood (Balčiauskas et al., 2012b).

The area consists of a polder system with artificially raised embankments to protect against high spring floods. The meadows are surrounded by ditches, overgrown by reeds and partially by shrubs (Figure 1). The main vegetation of the meadow consists of Poaceae and Cyperaceae plants. These flooded meadows were not cut during

FIGURE 1 Study site position in the Nemunas River Delta (between Nemunas (Atmata) and Skirvytė river branches) and habitat structure of the site. Red lines represent trap setting lines in 2008–2016. The diagonal line was operational in 2009 only

TABLE 1 Composition of the small mammal community in a seasonally flooded meadow at Rusnė (western Lithuania), 2008–2016 and trapping effort

										Total	
Species	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**N**	**%**
Sorex araneus[a]	35	42	31	2	44	9	14	9	7	193	14.2
Sorex minutus[a]	3	8	12	–	3	2	–	4	3	35	2.6
Neomys fodiens[a]	2	–	–	–	–	–	–	–	–	2	0.1
Apodemus agrarius[b]	22	60	193	124	57	17	55	53	63	644	47.4
Apodemus flavicollis[b]	–	–	–	–	3	–	–	–	–	3	0.2
Micromys minutus[b]	53	–	33	–	10	–	5	2	1	104	7.7
Microtus arvalis[c]	–	2	–	–	–	–	2	–	–	4	0.3
Microtus agrestis[c]	–	–	1	–	–	–	3	10	7	21	1.5
Microtus oeconomus[c]	46	102	30	14	67	5	7	37	–	308	22.7
Myodes glareolus[d]	–	–	13	2	2	1	10	13	3	44	3.2
Arvicola amphibius[c]	–	–	1	–	–	–	–	–	–	1	0.1
Total, *N*	161	214	314	142	186	34	96	128	84	1,359	100
No of species	6	5	8	4	7	5	7	7	6	11	
Shannon's *H*	2.10	1.73	1.85	0.67	2.03	1.80	1.98	2.19	1.33	2.13	
Simpson's *c*	0.26	0.35	0.41	0.77	0.28	0.35	0.37	0.28	0.58	0.30	
Trapping effort, trap lines	20	31	23	8	12	6	9	6	6	121	
Trapping effort, trap nights	750	1995	1525	600	750	450	681	450	450	7,651	

Notes. Diet preferences marked with superscripts: a—insectivores, b—granivores, c—herbivores, d—omnivores (according to Butet & Delettre, 2011; Churchfield & Rychlik, 2006; Zub et al., 2012; Pernetta, 1976). Shannon's H measures diversity of the small mammal community, Simpson's c the dominance. Trapping effort is expressed in trap nights

the investigation period, except in 2012–2013 when vegetation from the central part of the site was cut once during the summer of each year, though the surrounding reed belts were left untouched. Trapping was performed at a time when the cut surface had re-grown. Visual assessment of the habitat and measuring several variables, such as grass height, reedbed presence, shrub presence, distance to the water, main species of the vegetation at all of the trapping locations in 2011–2016, confirmed its uniformity (*unpublished data*).

2.2 | Small mammal trapping

Small mammals were trapped in 2008–2016. In 2011 and 2013–2016, trapping occurred once at the end of September/beginning of October. In the other years, there were two or three trapping sessions (July–September). In the years with several trapping sessions, there were no shifts in the numbers of the two most numerous small mammal species between the trapping sessions, so the data were pooled. Each year, we used 6–31 lines of 25 snap traps, each set 5 m apart, the number of lines depending on the number of trapping sessions (Table 1). We positioned the traps according to the perimeter of the site in all years, the trap lines being close to drainage ditches (2–10 m) and adjacent reed belts. In 2009, traps were additionally set on a diagonal transect (Figure 1). Traps were set for three days, checked once a day, and baited with bread crust and sunflower oil. The total trapping effort was 7,651 trap nights, and 1,359 individuals of 11 species were captured (Table 1). Presented in the Supporting information Table S1, relative abundance was expressed as standard capture rates to number of animals/100 trap nights. Most of the registered species were typical for the region. In Lithuania, common vole (*Microtus arvalis*), common shrew (*Sorex araneus*), *M. glareolus*, *A. flavicollis*, striped field mouse (*Apodemus agrarius*), and pygmy shrew (*Sorex minutus*) are typical meadow species.

Species were identified morphologically, with specimens of *Microtus* voles identified by their teeth. Juveniles, subadults, and adults were identified under dissection, based on body weight, the status of sex organs and atrophy of the thymus, the latter of which decreases with animal age (Balčiauskas, Balčiauskienė, & Janonytė, 2012a). After cleaning using *Dermestes* beetles, skulls were deposited at the Laboratory of Mammalian Ecology of the Nature Research Centre (Vilnius, Lithuania).

2.3 | Stable isotope analysis

To test predictions P2 and P3, hair samples were collected in 2015 from 81 individuals of the seven small mammal species for stable isotope analysis (Table 2). We clipped off a tuft of hair from between the shoulders of each specimen and stored it dry in separate bags. Scissored samples were weighed with a microbalance and packed in tin capsules, and stable isotope analysis was then carried out. Carbon and nitrogen stable isotope ratios were measured using an elemental analyzer (EA) (Flash EA1112) coupled to an isotope ratio mass spectrometer (IRMS) (Thermo Delta V Advantage) via a ConFlo III interface (EA-IRMS).

Carbon and nitrogen isotope data are reported as δ X values (where X represents the heavier isotope ^{13}C or ^{15}N) or differences from given standards, expressed in parts per thousand (‰), and are calculated according to the formula:

$$\delta X = [R_{sample}/R_{standard} - 1] \times 1000.$$

where R_{sample} = $^{13}C/^{12}C$ or $^{15}N/^{14}N$ of the sample, $R_{standard}$ = $^{13}C/^{12}C$ or $^{15}N/^{14}N$ of the standard.

Reference materials Caffeine IAEA-600 ($\delta^{13}C$ = −27.771 ± 0.043‰, $\delta^{15}N$ = 1 ± 0.2‰) and oil NBS-22 IAEA ($\delta^{13}C$ = −30.031 ± 0.043‰) provided by the International Atomic Energy Agency (IAEA) were used as standards for calibration of the reference gases (CO_2 and N_2). EMA P2 (Elemental Microanalysis, $\delta^{13}C$ = −28 ± 0.1‰, $\delta^{15}N$ = −2 ± 0.2‰) was selected as a laboratory working standard. Repeated analysis of this reference material gave a standard deviation of less than 0.08‰ for carbon and 0.2‰ for nitrogen (Balčiauskas et al., 2016).

2.4 | Data analysis

The diversity of the small mammal community was expressed using the Shannon–Wiener diversity index, H, on the base of $\log_2$ (Krebs, 1999), while dominance was expressed using the Simpson's index c (Golet et al., 2013; Krebs, 1999; Zhang et al., 2007). Diversity of the community was compared to other habitats and territories of different size in Lithuania, data from Balčiauskas and Juškaitis (1997).

We checked if there was a correlation between diversity and *A. agrarius* dominance (this a generally uncommon species in the country, but strongly dominant during most of the investigation). Dominance was calculated as a percentage of the total number of trapped individuals. Pearson's *r* was used as dominance values were distributed normally.

Prediction P1 was tested according to the rule of equal representation of functional groups (insectivores, granivores, herbivores, and omnivores) in a small mammal community (Fox, 1987). Accordingly, if the difference between the numbers of species trapped in these four groups in any year is >1, the state of the community is considered unfavorable. The distribution of favored and unfavored states of the small mammal communities in the Rusnė flooded meadow is presented in Supporting information Table S2. The pool of species in the area was insectivores (*I*) = 3, granivores (*G*) = 3, herbivores (*H*) = 4, and omnivores (*O*) = 1. Consequently,

TABLE 2 Small mammal samples used for stable isotope analysis from a seasonally flooded meadow at Rusnė, 2015 (animal age and sex in insectivores not always known due to self-digestion* of the internal organs)

Species	*N*	Males	Females	Adults	Subadults	Juveniles
Sorex araneus	5	2	2	–	1	–
Sorex minutus	3	–	–	–	–	–
Apodemus agrarius	12	8	4	1	5	6
Micromys minutus	1	–	1	–	–	1
Microtus agrestis	11	2	9	3	3	5
Microtus oeconomus	34	14	20	15	7	12
Myodes glareolus	15	10	5	2	2	11

*In shrews after trapping with snap traps, digestion processes do not stop, thus resulting in abdominal organs, including testes, uterus, and ovaries, being unavailable for sex determination. Self-digestion of *gl. thymus* does not allow for age estimation of an individual. For the other species, self-digestion is not characteristic.

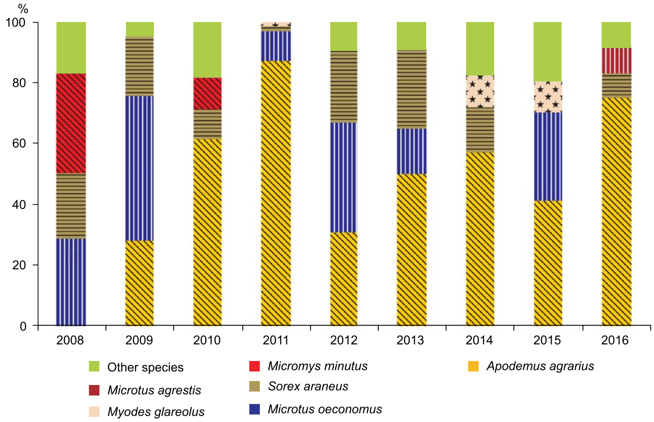

FIGURE 2 Temporal changes in the numbers of small mammal species in the Rusnė flooded meadow (less numerous species pooled). Dietary groups indicated by hatching (vertical—herbivores, diagonal—granivores, horizontal—insectivores) and pattern (stars—omnivores)

the probability of their presence in the community was $I = 0.273$, $G = 0.273$, $H = 0.364$, and $O = 0.090$, respectively. We calculated the expected number of species in the functional groups for every year of the investigation. The significance between expected and observed numbers was tested using a chi-square test. Representation of the functional groups in the community was also evaluated using the three most abundant species in any year (Figure 2).

The δ^{13}C and δ^{15}N values in the samples were expressed as arithmetic mean ± 1 *SE*. Normality of the δ^{15}N and δ^{13}C values was evaluated using Kolmogorov–Smirnov test. Based on conformity to normal distribution, parametric tests were used. Main-effects ANOVA was used to find the relationship of dietary group, species, age, and sex of individuals to paired δ^{15}N and δ^{13}C distribution, using Hotelling's two sample T^2 test for significance.

The influences of species, as well as intraspecific differences (between males and females, and between the three age groups), on the carbon and nitrogen stable isotope values were tested with parametric ANOVA, using Wilk's lambda test for significance. Differences between groups were evaluated with post hoc Tukey test.

Isotopic niches of species, as central ellipses, were calculated using SIBER (Jackson, Inger, Parnell, & Bearhop, 2011) using R ver. 3.5.0 (https://cran.r-project.org/bin/windows/base/rdevel.html) for the five most numerous small mammal species, having five or more individuals investigated for δ^{15}N and δ^{13}C. Positions of seven small mammal species, including those with sample size $n < 5$, in the isotopic biplot were shown using SigmaPlot ver. 12.5. All other calculations were performed using Statistica for Windows ver. 6.

3 | RESULTS

3.1 | Diversity of small mammals in the flooded meadow

Eleven species of small mammals were trapped in 2008–2016. During the investigation, the granivorous *A. agrarius* dominated the community most frequently (six out of nine years), while the herbivorous root vole (*Microtus oeconomus*) dominated in two years and the granivorous harvest mouse (*Micromys minutus*) in one year (Figure 2). In addition to these, three further species had relatively high abundance, these being the insectivorous *S. araneus* (all years, 2008–2016), the omnivorous *M. glareolus* (2014 and 2015), and the herbivorous short-tailed vole (*Microtus agrestis*) in 2016 (Supporting information Table S1).

Diversity of the small mammal community was high (Shannon's $H = 2.13$, variation between years from the minimum of $H = 0.67$ in 2011 to the maximum $H = 2.19$ in 2015). Dominance was low, Simpson's $c = 0.30$, with a maximum in 2011 when *A. agrarius* was absolute dominant in the community, comprising 87.3% of all trapped individuals (Table 1).

An increasing dominance of *A. agrarius* was negatively related to the diversity of the small mammal community ($r = -0.74$, $n = 9$, $p = 0.02$). In the years of the strongest dominance of *A. agrarius*, the small mammal community consisted of 4–5 species, with a low abundance or absence of *M. minutus*, a species belonging to the same granivorous group (Table 1).

3.2 | Temporal changes

Throughout the investigation, the composition of the small mammal community followed the expected numbers of species in functional groups (differences from the expected numbers were not significant). However, in five out of the nine years, the state of the small mammal community was unfavored. Favored states were found in 2011, 2013, 2015, and 2016, when numbers of species with similar dietary preferences were present according to the assembly rule (Supporting information Table S2). Unfavored states were registered when high numbers of insectivores were present in 2008, granivores in 2012, and herbivores in 2010 and 2014—that is, three functional groups had chances to be over-rich in species.

In eight out of the nine study years, the three most abundant species were characterized by different diet preferences. Only in 2010 were two granivorous rodents (*A. agrarius*, *M. minutus)* dominant (Figure 2). In 2014 and 2016, years of low abundance or absence of *M. oeconomus*, *M. agrestis*, and *M. glareolus* were both recorded in high numbers. The herbivores *M. arvalis* and the water vole (*Arvicola amphibius*), as well as the granivorous *A. flavicollis*, occurred in low abundances (Table 1).

Thus, based on the frequent deviations from the species assembly rule, P1 prediction was not fully confirmed, but a change in small mammal numbers over time (shifting dominance) was clearly demonstrated.

3.3 | Isotopic partitioning

Both δ^{15}N and δ^{13}C values in *S. araneus*, *A. agrarius*, *M. oeconomus*, *M. agrestis*, and *M. glareolus* were distributed normally (Kolmogorov–Smirnov test, NS). MANOVA revealed that small mammal species had a significant effect (Hotelling's $T^2 = 0.13$, $p = 0.022$) on the paired δ^{15}N and δ^{13}C distribution, but not dietary group or age or sex of individuals ($T^2 = 0.00$, $T^2 = 0.07$, $T^2 = 0.003$, all NS, respectively). Such model explained 34% of variation of δ^{15}N ($r^2 = 0.34$, $F_{6,65} = 7.00$, $p < 0.0001$) and 48% of variation of δ^{13}C ($r^2 = 0.48$, $F_{6,65} = 11.78$, $p < 0.0001$).

Performing species-based analysis, we found significant differences in the distribution of stable isotopes in the hair of small mammals of different species in 2015 (Wilk's lambda = 0.24, $F_{12,146} = 12.74$, $p < 0.0001$). Species had a significant effect on the differences of δ^{15}N and δ^{13}C ($F_{6,74} = 16.64$ and $F_{6,74} = 15.38$, both $p < 0.0001$).

3.4 | Interspecific differences in dietary space

The range of stable isotope values, though overlapping, showed a separation of several species (Figure 3, Supporting information Table S3) and functional groups (Supporting information Table S4). According to δ^{15}N, three groups were identified: the highest average isotope values being in the insectivorous shrews, with medium values in granivorous rodents (28.9% less than shrews) and the lowest values in herbivorous voles (30.2% less than granivorous mice). The omnivorous *M. glareolus* in this respect was closer to the group of granivores species (difference 5.1%).

According to δ^{13}C, lower values were registered in herbivorous voles and omnivorous *M. glareolus*, with higher values in shrews and mice (Figure 3a). The difference between average δ^{13}C values in granivores and herbivores was 5.6%, while between granivores and omnivores it was 5.9% and between omnivores and insectivores 4.3%. However, the difference between herbivores and omnivores was just 0.3% (Supporting information Table S4).

The dietary niches of the most abundant species (core ellipses in the isotopic space) were separated and did not intersect (Figure 3b), the only exception being *M. oeconomus* and *A. agrarius*, these having overlap in core ellipses of <2%. Thus, in this limited area, sympatric species of small mammals are separated dietary, confirming P2 prediction.

3.5 | Intraspecific differences in dietary space

Differences in the stable isotopes in the hair of male and female small mammals were not significant in general for δ^{15}N ($F_{1,10} = 1.36$, $p = 0.27$) or δ^{13}C ($F_{1,10} = 1.51$, $p = 0.31$), nor in some separate species (Supporting information Figure S1). No significant differences between stable isotope values were found between age groups in *A. agrarius*, *M. glareolus*, and *M. agrestis* (Figure 4a–c). Thus, prediction P3 for most of the analyzed species was not confirmed.

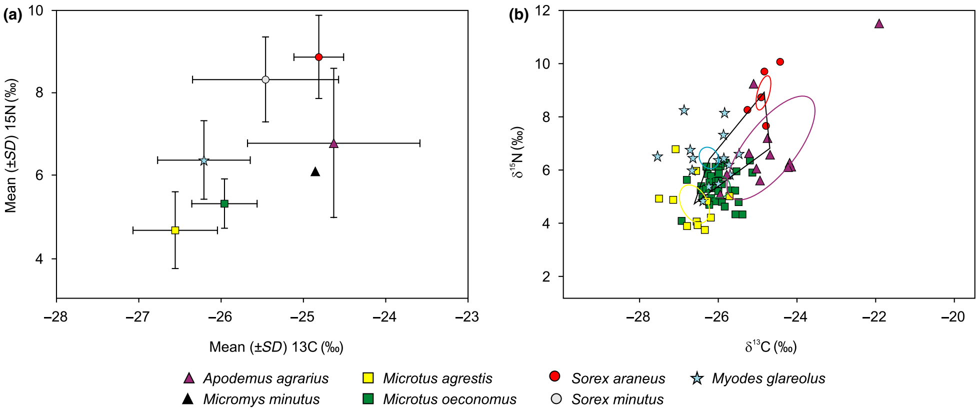

FIGURE 3 Distribution of small mammal species from the seasonally flooded meadow in Rusnė according to isotopic values (a) and central ellipses of species (b) in the isotopic space, representing fundamental niches. Bars represent 1 *SD* of the mean. Insectivorous species are shown by circles, granivorous by triangles, herbivorous by squares, and omnivorous species by stars. Central ellipses include 1 *SD* of the mean, or ~40% of data. The central ellipse of *Sorex araneus* is shown in red, *Apodemus agrarius* in magenta, *Microtus agrestis* in yellow, *Microtus oeconomus* in green, and that of *Myodes glareolus* in blue. The polygon (black line) represents the central isotopic niche of the small mammal community

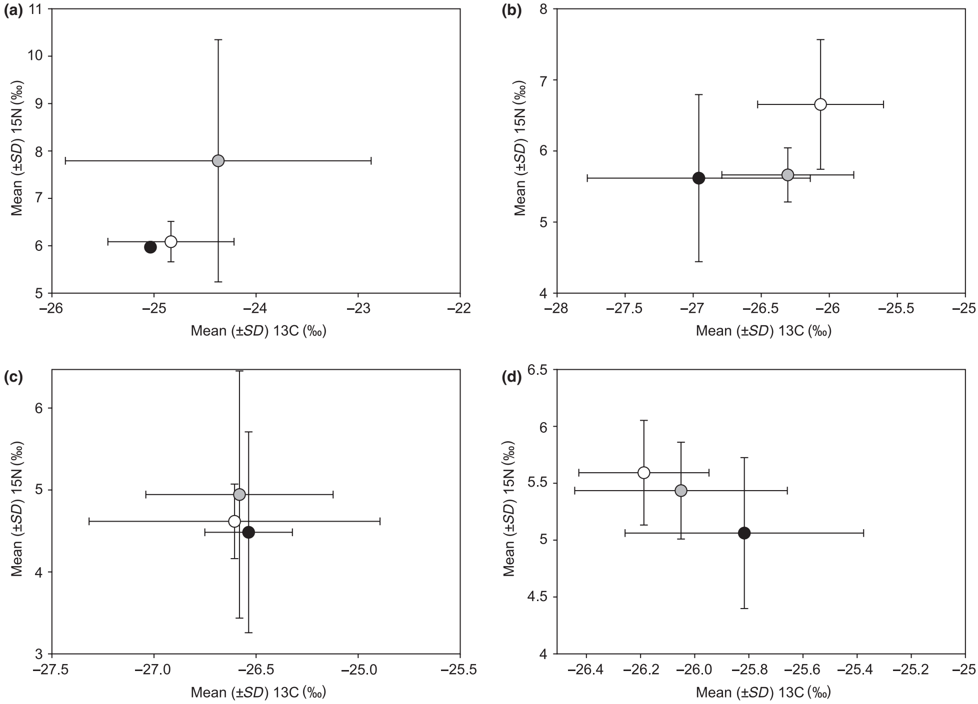

FIGURE 4 Intraspecific differences in the stable isotope values in the hair of young, subadult, and adult small mammals: a—*Apodemus agrarius*, b—*Myodes glareolus*, c—*Microtus agrestis*, d—*Microtus oeconomus*, black circles—adult, gray circles—subadult, white circles—young animals. Differences between young and adult animals in *M. oeconomus* were significant for δ^{13}C and had a trend for δ^{15}N ($p = 0.054$)

In *M. oeconomus*, differences in the stable isotopes in the hair of young, subadult, and adult small mammals were significant for δ^{13}C ($F_{2,31} = 3.34$, $p = 0.048$) and near-significant for δ^{15}N ($F_{2,31} = 3.21$, $p = 0.054$) (Figure 4d). However, the difference expressed in percentage was not large: juveniles of *M. oeconomus* were characterized by 1.4% lower δ^{13}C than adult animals and 10.5% higher δ^{15}N.

4 | DISCUSSION

We analyzed how several small mammal species, representing insectivores, granivores, herbivores, and omnivores, share a seasonally flooded meadow of limited size. With the re-occupation of the habitat after the spring flood, spatial arrangement may "pack" species of small mammals tightly, high floods giving chances to uncommon species to establish (Balčiauskas et al., 2012b). We identified separation of dominant species by time and by isotopic partitioning of sympatric species, but not by intraspecific differences in diet (with one exception). Because flooded meadows are a resource-rich habitat (Marques et al., 2015; Wijnhoven, Van Der Velde, Leuven, & Smits, 2005), unfavored small mammal community states with increased competition of several species from the same group were possible in five out of the nine years. Core areas of the three most abundant species in the isotopic space were separated, showing their dependence on different dietary resources.

4.1 | Small mammal diversity in the flooded areas

In general, higher species diversities are characteristic of larger areas (Balčiauskas & Juškaitis, 1997), but similar patterns are also found in seasonally flooded sites. For example, in the floodplains of the Sava River, 23 small mammal species were registered (Crnobrnja-Isailović et al., 2015), and in a much bigger area of the flooded Narewka River valley in Poland, the diversity was higher, with $H = 2.46$ and 11 species registered (Zub et al., 2012). The small mammal diversity in Rusnė did not differ from the bigger floodplains of the Vltava ($H = 2.18$, 8 species) and Danube ($H = 2.21$, 9 species) rivers (Bohdal, Navratil, & Sedlaček, 2016; Miklós, Žiak, & Hulejová, 2015).

Our diversity index ($H = 2.13$) was greater than that found in 95 out of 125 small mammal trapping sites across Lithuania, regardless of the size of these territories, which were in most cases significantly larger. Only in eight territories was the number of registered small mammal species larger than in the flooded meadow at Rusnė (re-calculated from Balčiauskas & Juškaitis, 1997).

Of note is a new small mammal species for the Baltic countries. Mediterranean shrew (*Neomys anomalus*) was found in flooded meadows at Rusnė (<100 m from the investigated site) living sympatrically with three other shrew species, water shrew (*Neomys fodiens*), *S. araneus*, and *S. minutus* (Balčiauskas & Balčiauskienė, 2012). Two other small mammal species that are uncommon in Lithuania, namely *M. oeconomus* and *M. minutus*, may also reach high densities in the Rusnė meadows (Balčiauskas et al., 2012b). These species are not common in Lithuania (Balčiauskas & Juškaitis, 1997; Balčiauskas, 2005; Balčiauskas, Čepukienė, & Balčiauskienė, 2017 and references therein), but are not rare in flooded meadows and river valleys in other European countries (Ambros et al., 2016; Crnobrnja-Isailović et al., 2015; Tast, 1966; Zub et al., 2012).

4.2 | Temporal changes in the dominant species

In the flooded meadow at Rusnė, high numbers of species sympatrically shared an area of limited size. Three species dominated during the nine years of investigation: the herbivorous *M. oeconomus* during two years, the granivorous *M. minutus* in one year and the granivorous *A. agrarius* in six years. An increase in *M. oeconomus* numbers was observed every fourth year (see Table 1), while *A. agrarius* dominated in the community for the last four years of the study period (2013–2016).

It has to be noted that floods are extreme environmental phenomena, not only causing small mammal mortality, but also changing the dominant species and the resulting organization of the entire community (Thibault & Brown, 2008). Seasonal floods do not only have negative or even catastrophic effects on small mammal communities (Andersen, Wilson, Miller, & Falck, 2000), but can also influence the diversity of such communities positively (Golet et al., 2013). Generally, an increase in diversity after disturbance is observed, though such a relationship is not always linear and straightforward (Mackey & Currie, 2001). We previously found that flood height was a key factor influencing diversity and dominance in the small mammal community in the Rusnė flooded meadows. After low-level floods, *A. agrarius* was the dominant species, while high-level floods increased the chances for other species to dominate the meadow (Balčiauskas et al., 2012b). This corresponds to the situation described by Brown et al. (2001), where environmental perturbations can fully reorganize ecosystems, exceeding the ecological tolerances of dominant or keystone species; though changes may be buffered due to the compensatory dynamics of complementary species. In the investigated area, the 2010 flood in particular was very high (Balčiauskas et al., 2012b), and it was in this year that the two most abundant species were granivores *A. agrarius* and *M. minutus*. *A. agrarius* was shown to be the best colonizer of previously flooded areas within agricultural land (Zhang et al., 2007).

However, in an earlier (1981–1990) long-term study of small mammals in eastern Lithuania, a different pattern of dominance was observed. In meadows, different dominant species were observed, namely *M. glareolus*, *M. arvalis*, and *S. araneus*, while *A. agrarius* numbers were always low (3.2% out of 2,346 individuals trapped) (Balčiauskas, 2005).

Thus, our recorded dominance of *A. agrarius* in the flooded meadow in six out of the nine years is not typical for Lithuania. There is no previous record of such dominance during earlier decades in various investigated habitats in the country (Balčiauskas, 2005; Balčiauskas et al., 2017; Balčiauskas & Juškaitis, 1997; Šinkūnas & Balčiauskas, 2006).

4.3 | Diet differences and favored states

Diet differences of small mammals form the basis of their community structure. Insectivores, granivores, herbivores, and omnivores may form "favored states" if "each species entering a community will be drawn from a different functional group… until each group is represented before the cycle repeats" (Fox, 1987; Kelt, Taper, & Meserve, 1995). This pattern has been observed in different communities of small mammals (Belyea & Lancaster, 1999; Brown, Fox, & Kelt, 2000; Eccard & Ylönen, 2003; Fox & Brown, 1993; Fox & Kirkland, 1992; Kelt et al., 1995; Rodríguez & Ojeda, 2013) and in various habitats (i.e., Zub et al., 2012; Golet et al., 2013; Balestrieri et al., 2017; Ambros et al., 2016; Luza, Gonçalves, Pillar, & Hartz, 2016; Ważna, Cichocki, Bojarski, & Gabryś, 2016). Exceptions however are also known (Jánová, Heroldová, & Čepelka, 2016; Marques et al., 2015).

Several previous investigations have also confirmed favored states of small mammal communities in Lithuania (i.e., Balčiauskas & Juškaitis, 1997; Balčiauskas, 2005; Šinkūnas & Balčiauskas, 2006; Balčiauskas et al., 2017). However, in our flooded meadow, the community of small mammals was in an unfavored state (sensu Fox, 1987) in five of the nine years, and in one year, the two most numerous species, namely *A. agrarius* and *M. minutus*, were both granivores. According to Tulis et al. (2016), the negative interaction of *A. agrarius* occurs mostly with *A. flavicollis*, *M. glareolus*, *S. araneus*, and *M. minutus*. Hence, it is unusual to observe a high number of *A. agrarius* and *M. minutus* simultaneously.

One possible explanation at this locality lies in the abundance of a prevailing lush herbaceous vegetation (Wijnhoven et al., 2005) and of reed seeds at the flooded sites (Marques et al., 2015). Alternatively, the changing structure of the small mammal community as it reoccupied the vacant area after a particularly high flood may also explain this unusual co-occurrence.

4.4 | Isotopic partitioning

We expected that the tight packing of sympatric species and their segregation in dietary space would be reflected by stable isotope values. Testing two predictions, we found that isotopic partitioning may have helped maintain a high diversity of small mammals in the seasonally flooded meadow. Species were segregated in dietary space (confirming prediction P2), as was shown by analysis of stable isotopes from their hair. We interpret nearly full separation of the central ellipses as separation in dietary space. The only overlap in central ellipses, being less than 2%, was that between *A. agrarius* (dominant species in most years) and *M. oeconomus*.

Diversity (but not abundance) of resources in a limited area presumably should also be limited, putting constraint on the differences in δ^{15}N and, even more, in δ^{13}C values. While differences in δ^{15}N between insectivores, herbivores, and granivores were nearly 30%, differences in δ^{13}C were a mere 5%. Thus, we have to interpret dietary separation with caution, possibly because of territorial limitation.

The widest trophic niche among the small mammals was occupied by *A. agrarius*, as the variance of stable isotope values in their hair was highest (see Figure 3a and Supporting information Table S3) and the core area largest (Figure 3b). A wider trophic niche supports stability in a species (Bearhop, Adams, Waldron, Fuller, & MacLeod, 2004; Wood et al., 2017), enabling the domination of *A. agrarius* in the area of investigation. We did not find intraspecific differences of stable isotope values in most of the investigated species (prediction P3 not confirmed), with some trend in *M. oeconomus* age groups only.

Isotopic partitioning of small mammal species is characteristic in other cases of limited space, such as under snow cover (Calandra et al., 2015; Merwe & Hellgren, 2016). The segregation of the isotopic niche spaces of small mammals, minimizing interspecific competition, allows sympatric species to coexist (Baltensperger et al., 2015), especially in grasslands, where small mammals are more plastic in their dietary preferences (Symes et al., 2013).

However, we found no other studies for comparison with regard to isotopic partitioning in small mammal species in a small area equivalent to the Rusnė flooded meadow. Although intraspecific dietary separation was found in *A. flavicollis* and *M. glareolus* living in the territory of a great cormorant colony, we interpret this as competition for scarce food resources and as adults feeding in the best habitats (Balčiauskas et al., 2016 and references therein). We suppose that abundant and diverse food in the cyclic habitat of the flooded meadow allows most species to avoid intraspecific competition. As for *M. oeconomus*, it is a relatively new species in Lithuania, arriving only about half a century ago (Balčiauskas, Balčiauskienė, & Baltrūnaitė, 2010), and thus, it may have a different strategy of habitat use.

5 | CONCLUSIONS AND SIGNIFICANCE

We found that the small mammal community in the restricted area of flooded meadow maintained a high species diversity despite a cyclic stressor (flood) due to isotopic partitioning (segregation in dietary space) and by changes in their number over time (shifting dominance). The shifting of dominant species maintains long-term diversity, reflecting the differing resilience of various species to the floods, while separation in dietary space most probably only works at the level of the current year. In most years, the three most abundant species represented each of the different functional groups, insectivores, granivores, herbivores, and omnivores. However, in five of the nine years, the community was in an unfavored state. Segregation of species in dietary space was confirmed by stable isotopes from their hair, with the only overlap in central ellipses occurring between *A. agrarius* (dominant in most years) and *M. oeconomus*. The dominant species, *A. agrarius*, was characterized by the widest diet.

In the future, with respect to climate change and the resultant expected increases in extreme flood events in northern Europe (Reader et al., 2014) and the arrival of new species due to changes in distribution ranges and consequent changes to communities and food webs (Baltensperger et al., 2015), knowledge of the formation of small mammal communities may help in the prognosis of ecosystem changes and predicting at-risk species.

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CONFLICT OF INTEREST

None declared.

AUTHORS' CONTRIBUTIONS

LB1 formulated the research idea, did statistical analysis, and drafted the manuscript; LB1, LB2, and MJ trapped small mammals; LB2 identified species, performed literature overview, and revised all manuscript versions; RS and MJ performed stable isotope analysis. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data from this study (stable isotope raw data matrix) available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.2rc8s7m.

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REFERENCES

Ambros, M., Baláz, I., Klimant, P., Tulis, F., Dudich, A., Stollmann, A., … Horváth, G. (2016). The occurrence of Pannonian root vole (*Microtus oeconomus mehelyi*) in small mammals' communities in Danubian Plain. *Folia Oecologica*, *43*, 83–88.

Andersen, D. C., Wilson, K. R., Miller, M. S., & Falck, M. (2000). Movement patterns of riparian small mammals during predictable floodplain inundation. *Journal of Mammalogy*, *81*, 1087–1099. https://doi.org/10.1644/1545-1542(2000)081<1087:MPORSM>2.0.CO;2

Balčiauskas, L. (2005). Results of the long-term monitoring of small mammal communities in the Ignalina Nuclear Power Plant Region

(Drūkšiai LTER site). *Acta Zoologica Lituanica*, *15*, 79–84. https://doi.org/10.1080/13921657.2005.10512378

Balčiauskas, L., & Balčiauskienė, L. (2012). Mediterranean water shrew, *Neomys anomalus* Cabrera, 1907 – a new mammal species for Lithuania. *North-Western Journal of Zoology*, *8*, 367–369.

Balčiauskas, L., Balčiauskienė, L., & Baltrūnaitė, L. (2010). Root vole, *Microtus oeconomus*, in Lithuania: Changes in distribution range. *Folia Zoologica*, *59*, 267–277.

Balčiauskas, L., Balčiauskienė, L., & Janonytė, A. (2012a). Reproduction of the root vole (*Microtus oeconomus*) at the edge of its distribution range. *Turkish Journal of Zoology*, *36*, 668–675.

Balčiauskas, L., Balčiauskienė, L., & Janonytė, A. (2012b). The influence of spring floods on small mammal communities in the Nemunas River Delta, Lithuania. *Biologia*, *67*, 1220–1229.

Balčiauskas, L., Čepukienė, A., & Balčiauskienė, L. (2017). Small mammal community response to early meadow–forest succession. *Forest Ecosystems*, *4*, 11. https://doi.org/10.1186/s40663-017-0099-6

Balčiauskas, L., & Juškaitis, R. (1997). Diversity of small mammal communities in Lithuania (1. A review). *Acta Zoologica Lituanica*. *Biodiversity*, *7*, 29–45.

Balčiauskas, L., Skipitytė, R., Jasiulionis, M., Balčiauskienė, L., & Remeikis, V. (2018). Immediate increase in isotopic enrichment in small mammals following the expansion of a great cormorant colony. *Biogeosciences*, *15*, 3883–3891. https://doi.org/10.5194/bg-15-3883-2018

Balčiauskas, L., Skipitytė, R., Jasiulionis, M., Trakimas, G., Balčiauskienė, L., & Remeikis, V. (2016). The impact of Great Cormorants on biogenic pollution of land ecosystems: Stable isotope signatures in small mammals. *Science of the Total Environment*, *565*, 376–383. https://doi.org/10.1016/j.scitotenv.2016.04.185

Balestrieri, A., Remonti, L., Morotti, L., Saino, N., Prigioni, C., & Guidali, F. (2017). Multilevel habitat preferences of *Apodemus sylvaticus* and *Clethrionomys glareolus* in an intensively cultivated agricultural landscape. *Ethology Ecology & Evolution*, *29*, 38–53.

Baltensperger, A. P., Huettmann, F., Hagelin, J. C., & Welker, J. M. (2015). Quantifying trophic niche spaces of small mammals using stable isotopes (δ15N and δ13C) at two scales across Alaska. *Canadian Journal of Zoology*, *93*, 579–588.

Barnosky, A. D., Hadly, E. A., Maurer, B. A., & Christie, M. I. (2001). Temperate terrestrial vertebrate faunas in North and South America: Interplay of ecology, evolution, and geography with biodiversity. *Conservation Biology*, *15*, 658–674. https://doi.org/10.1046/j.1523-1739.2001.015003658.x

Bearhop, S., Adams, C. E., Waldron, S., Fuller, R. A., & MacLeod, H. (2004). Determining trophic niche width: A novel approach using stable isotope analysis. *Journal of Animal Ecology*, *73*, 1007–1012.

Belyea, L. R., & Lancaster, J. (1999). Assembly rules within a contingent ecology. *Oikos*, *86*, 402–416. https://doi.org/10.2307/3546646

Bohdal, T., Navratil, J., & Sedlaček, F. (2016). Small terrestrial mammals living along streams acting as natural landscape barriers. *Ekologia (Bratislava)*, *35*, 191–204. https://doi.org/10.1515/eko-2016-0015

Brown, J. H., Fox, B. J., & Kelt, D. A. (2000). Assembly rules: Desert rodent communities are structured at scales from local to continental. *The American Naturalist*, *156*, 314–321. https://doi.org/10.1086/303385

Brown, J. H., Whitham, T. G., Ernest, S. M., & Gehring, C. A. (2001). Complex species interactions and the dynamics of ecological systems: Long-term experiments. *Science*, *293*, 643–650. https://doi.org/10.1126/science.293.5530.643

Butet, A., & Delettre, Y. R. (2011). Diet differentiation between European arvicoline and murine rodents. *Acta Theriologica*, *56*, 297–304. https://doi.org/10.1007/s13364-011-0049-6

Calandra, I., Labonne, G., Mathieu, O., Henttonen, H., Lévêque, J., Milloux, M. J., … Navarro, N. (2015). Isotopic partitioning by small mammals in the subnivium. *Ecology and Evolution*, *5*, 4132–4140. https://doi.org/10.1002/ece3.1653

Churchfield, S., & Rychlik, L. (2006). Diets and coexistence in Neomys and Sorex shrews in Białowieża forest, eastern Poland. *Journal of Zoology*, *269*, 381–390.

Crnobrnja-Isailović, J., Adrović, A., Ćaleta, M., Ćosić, N., Jelić, D., Kotrošan, D., & Sekulić, G. (2015). Fauna of the Riparian Ecosystems: Amphibians. In B. Reptiles, R. Mammals, & Milačič, (Eds.), *The Sava River* (pp. 401–435). Berlin, Heidelberg: Springer-Verlag.

Dueser, R. D., & Shuggart, H. H. (1979). Niche pattern in a forest-floor small-mammal fauna. *Ecology*, *60*, 108–118. https://doi.org/10.2307/1936473

Eccard, J. A., & Ylönen, H. (2003). Interspecific competition in small rodents: From populations to individuals. *Evolutionary Ecology*, *17*, 423–440. https://doi.org/10.1023/A:1027305410005

European Environment Agency (2002). Europe's biodiversity – biogeographical regions and seas. Retrieved from https://www.eea.europa.eu/publications/report_2002_0524_154909

Floods (2018). Nemuno deltos regioninis Parkas. Retrieved from http://www.nemunodelta.lt/16976/gamta/potvyniai.html

Fox, B. J. (1987). Species assembly and the evolution of community structure. *Evolutionary Ecology*, *1*, 201–213. https://doi.org/10.1007/BF02067551

Fox, B. J., & Brown, J. H. (1993). Assembly rules for functional groups in North American desert rodent communities. *Oikos*, *67*, 358–370. https://doi.org/10.2307/3545483

Fox, B. J., & Kirkland, G. L. (1992). An assembly rule for functional groups applied to North American soricid communities. *Journal of Mammalogy*, *73*, 491–503. https://doi.org/10.2307/1382015

Galetti, M., Rodarte, R. R., Neves, C. L., Moreira, M., & Costa-Pereira, R. (2016). Trophic niche differentiation in rodents and marsupials revealed by stable isotopes. *PLoS One*, *11*, e0152494. https://doi.org/10.1371/journal.pone.0152494

Golet, G. H., Hunt, J. W., & Koenig, D. (2013). Decline and recovery of small mammals after flooding: Implications for pest management and floodplain community dynamics. *River Research and Applications*, *29*, 183–194. https://doi.org/10.1002/rra.1588

Hallett, J. G. (1991). The structure and stability of small mammal faunas. *Oecologia*, *88*, 383–393. https://doi.org/10.1007/BF00317583

Hwang, Y. T., Millar, J. S., & Longstaffe, F. J. (2007). Do $\delta\ ^{15}$N and $\delta\ ^{13}$C values of feces reflect the isotopic composition of diets in small mammals? *Canadian Journal of Zoology*, *85*, 388–396.

Jackson, A. L., Inger, R., Parnell, A. C., & Bearhop, S. (2011). Comparing isotopic niche widths among and within communities: SIBER–Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology*, *80*, 595–602. https://doi.org/10.1111/j.1365-2656.2011.01806.x

Jánová, E., Heroldová, M., & Čepelka, L. (2016). Rodent food quality and its relation to crops and other environmental and population parameters in an agricultural landscape. *Science of the Total Environment*, *562*, 164–169.

Jorgensen, E. E. (2004). Small mammal use of microhabitat reviewed. *Journal of Mammalogy*, *85*, 531–539. https://doi.org/10.1644/BER-019

Kasper, C. B., Peters, F. B., Christoff, A. U., & de Freitas, T. R. O. (2016). Trophic relationships of sympatric small carnivores in fragmented landscapes of southern Brazil: Niche overlap and potential for competition. *Mammalia*, *80*, 143–152. https://doi.org/10.1515/mammalia-2014-0126

Kelt, D. A., Taper, M. L., & Meserve, P. L. (1995). Assessing the impact of competition on community assembly: A case study using small mammals. *Ecology*, *76*, 1283–1296. https://doi.org/10.2307/1940935

Krebs, C. J. (1999). *Ecological methodology* (2nd ed., p. 620). Menlo Park, CA: Addison-Wesley Educational Publishers Inc.

Kronfeld-Schor, N., & Dayan, T. (1999). The dietary basis for temporal partitioning: Food habits of coexisting *Acomys* species. *Oecologia*, *121*, 123–128. https://doi.org/10.1007/s004420050913

Luo, J. I. A., & Fox, B. J. (1996). Seasonal and successional dietary shifts of two sympatric rodents in coastal heathland: A possible mechanism for coexistence. *Austral Ecology*, *21*, 121–132. https://doi.org/10.1111/j.1442-9993.1996.tb00593.x

Luza, A. L., Gonçalves, G. L., Pillar, V. D., & Hartz, S. M. (2016). Processes related to habitat selection, diversity and niche similarity in assemblages of non-volant small mammals at grassland–forest ecotones. *Natureza & Conservação*, *14*, 88–98. https://doi.org/10.1016/j.ncon.2016.09.003

Mackey, R. L., & Currie, D. J. (2001). The diversity–disturbance relationship: Is it generally strong and peaked? *Ecology*, *82*, 3479–3492.

Marques, S. F., Rocha, R. G., Mendes, E. S., Fonseca, C., & Ferreira, J. P. (2015). Influence of landscape heterogeneity and meteorological features on small mammal abundance and richness in a coastal wetland system, NW Portugal. *European Journal of Wildlife Research*, *61*, 749–761. https://doi.org/10.1007/s10344-015-0952-2

Mathar, W., Kleinebecker, T., & Hölzel, N. (2015). Environmental variation as a key process of co-existence in flood-meadows. *Journal of Vegetation Science*, *26*, 480–491. https://doi.org/10.1111/jvs.12254

Merwe, J., & Hellgren, E. C. (2016). Spatial variation in trophic ecology of small mammals in wetlands: Support for hydrological drivers. *Ecosphere*, *7*, e01567.

Meserve, P. L. (1981). Resource partitioning in a Chilean semi-arid small mammal community. *The Journal of Animal Ecology*, *50*, 745–757.

Miklós, P., Žiak, D., & Hulejová, S. V. (2015). Community of small terrestrial mammals in Danubian inundation area in autumn 2013. *Folia Faunistica Slovaca*, *20*, 105–111.

Myllymäki, A., & Myllymaki, A. (1977). Interactions between the field vole *Microtus agrestis* and its microtine competitors in Central-Scandinavian populations. *Oikos*, *29*, 570–580. https://doi.org/10.2307/3543595

Pernetta, J. C. (1976). Diets of the Shrews *Sorex araneus* L. and *Sorex minutus* L. in Wytham Grassland. *The Journal of Animal Ecology*, *45*, 899–912.

Reader, H. E., Stedmon, C. A., & Kritzberg, E. S. (2014). Seasonal contribution of terrestrial organic matter and biological oxygen demand to the Baltic Sea from three contrasting river catchments. *Biogeosciences*, *11*, 3409–3419. https://doi.org/10.5194/bg-11-3409-2014

Rodríguez, D., & Ojeda, R. A. (2013). Scaling coexistence and assemblage patterns of desert small mammals. *Mammalian Biology-Zeitschrift Für Säugetierkunde*, *78*, 313–321. https://doi.org/10.1016/j.mambio.2013.04.003

Scheffer, M., Carpenter, S. r., Lenton, T. m., Bascompte, J., Brock, W., Dakos, V., … Vandermeer, J. (2012). Anticipating critical transitions. *Science*, *338*, 344–348. https://doi.org/10.1126/science.1225244

Schoener, T. W. (1974). Resource partitioning in ecological communities. *Science*, *185*, 27–39. https://doi.org/10.1126/science.185.4145.27

Shiels, A. B., Flores, C. A., Khamsing, A., Krushelnycky, P. D., Mosher, S. M., & Drake, D. R. (2013). Dietary niche differentiation among three species of invasive rodents (*Rattus rattus*, *R. exulans*, *Mus musculus*). *Biological Invasions*, *15*, 1037–1048.

Šinkūnas, R., & Balčiauskas, L. (2006). Small mammal communities in the fragmented landscape in Lithuania. *Acta Zoologica Lituanica*, *16*, 130–136. https://doi.org/10.1080/13921657.2006.10512721

Sozio, G., & Mortelliti, A. (2016). Empirical evaluation of the strength of interspecific competition in shaping small mammal communities in fragmented landscapes. *Landscape Ecology*, *31*, 775–789. https://doi.org/10.1007/s10980-015-0286-1

Symes, C. T., Wilson, J. W., Woodborne, S. M., Shaikh, Z. S., & Scantlebury, M. (2013). Resource partitioning of sympatric small mammals in an African forest-grassland vegetation mosaic. *Austral Ecology*, *38*, 721–729. https://doi.org/10.1111/aec.12020

Tast, J. (1966). The root vole, *Microtus oeconomus* (Pallas), as an inhabitant of seasonally flooded land. *Annales Zoologici Fennici*, *3*, 127–171.

Thibault, K. M., & Brown, J. H. (2008). Impact of an extreme climatic event on community assembly. *Proceedings of the National Academy of Sciences*, *105*, 3410–3415. https://doi.org/10.1073/pnas.0712282105

Tulis, F., Ambros, M., Baláz, I., Ziak, D., Sládkovicová, V. H., Miklós, P., … Horváth, G. (2016). Expansion of the Striped field mouse (*Apodemus agrarius*) in the south-western Slovakia during 2010–2015. *Folia Oecologica*, *43*, 64–73.

Ważna, A., Cichocki, J., Bojarski, J., & Gabryś, G. (2016). Impact of sheep grazing on small mammals diversity in lower mountain coniferous forest glades. *Applied Ecology and Environmental Research*, *14*, 115–127. https://doi.org/10.15666/aeer/1403_115127

Wijnhoven, S., Smits, A. J. M., Van der Velde, G., & Leuven, R. S. E. W. (2006). Modelling recolonisation of heterogeneous river floodplains by small mammals. *Hydrobiologia*, *565*, 135–152. https://doi.org/10.1007/s10750-005-1910-x

Wijnhoven, S., Van Der Velde, G., Leuven, R. S., & Smits, A. J. (2005). Flooding ecology of voles, mice and shrews: The importance of geomorphological and vegetational heterogeneity in river floodplains. *Acta Theriologica*, *50*, 453–472. https://doi.org/10.1007/BF03192639

Wilson, A. C., Fenton, B., Malloch, G., Boag, B., Hubbard, S., & Begg, G. S. (2014). Coexisting small mammals display contrasting strategies for tolerating instability in arable habitat. *European Journal of Wildlife Research*, *60*, 811–820. https://doi.org/10.1007/s10344-014-0852-x

Wood, C. M., McKinney, S. T., & Loftin, C. S. (2017). Intraspecific functional diversity of common species enhances community stability. *Ecology and Evolution*, *7*, 1553–1560. https://doi.org/10.1002/ece3.2721

Zhang, M., Wang, K., Wang, Y., Guo, C., Li, B., & Huang, H. (2007). Recovery of a rodent community in an agro-ecosystem after flooding. *Journal of Zoology*, *272*, 138–147. https://doi.org/10.1111/j.1469-7998.2006.00248.x

Zub, K., Jędrzejewska, B., Jędrzejewski, W., & Bartoń, K. A. (2012). Cyclic voles and shrews and non-cyclic mice in a marginal grassland within European temperate forest. *Acta Theriologica*, *57*, 205–216. https://doi.org/10.1007/s13364-012-0072-2

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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PAPER VIII

Seasonal and daily activity patterns of mammals in the colony of cormorants

Jasiulionis, M., Balčiauskas, L.

Unpublished manuscript (2020)

Seasonal and daily activity patterns of mammals in the colony of great cormorants

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Abstract

Despite extreme changes of ecosystems made by breeding colonies of great cormorants (*Phalacrocorax carbo*), these territories are still used by mammals. We present results of the analysis of mammal seasonal and daily activity patterns, registered by camera traps in two colonies of the great cormorants in Lithuania.

Red foxes and raccoon dogs mainly visited colonies in the cormorant breeding time, April to July. In the inland colony of great cormorants in Lukštas Lake, average red fox relative shooting frequency in cormorant breeding time considerably exceeded that in non-breeding time (on average, 41.8 and 5.9 photos/100 days respectively). In the peninsular colony of great cormorants in Juodkrantė average relative shooting frequency of red fox in the breeding time was 6.2 versus 2.9 photos/100 days in non-breeding time, relative shooting frequencies of raccoon dog were 50.0 versus 1.3 photos/100 days, respectively. All these differences are significant.

Daily activity patterns of wild boar and red fox in both colonies, as well as activity patterns of raccoon dog in Lukštas were significantly related to the activity of cormorants.

Keywords:

Camera traps, cormorant colony, mammals, activity differences

Introduction

Great cormorants are able to induce drastic changes of the ecosystem in the territory of the breeding colonies (Kameda et al. 2006). A single bird consumes 400 g fish per day and deposits 20–50 g of faeces. Great cormorants spent about 20 h daily in breeding colonies and about 80% of faeces are deposited there (Klimaszyk and Rzymsky 2016). Deposited faeces overload the ecosystem with N and P by 10^4 to 10^5 times (Garcia et al. 2011). Nutrients transported by breeding birds from water to land ecosystems transform the composition of vegetation, thereby changing hiding and feeding conditions of mammals. Changed chemical properties of soil affect plants (Anderson and Polis 1999), lichens (Zolkos et al. 2013), myxomycetes (Adamonytė et al. 2012), fungal communities (Kutorga et al. 2013), herpetofauna (Kohno and Ota 1991), insects and lizards (Polis and Hurd 1996). Previous studies disclosed how cormorant colonies are reducing relative abundance, diversity and body condition of small mammals, as well as changing their population structure (Balčiauskienė et al. 2014, Balčiauskas et al. 2015). Influence of a great cormorant colony on skull morphometry (Balčiauskienė et al. 2015), stable isotope signatures (Balčiauskas et al. 2016, Balčiauskas et al. 2018) and accumulation of chemical elements (Jasiulionis et al. 2018) in small mammals also were observed.

Camera trap based methods are financially cost-effective, they save time resources and are non-invasive (Wearn and Glover-Kapfer 2019). Data collected by camera traps are comparable between different places and in time (Silveira et al. 2003, Bondi et al. 2010). Furthermore, this method enables to record many individual animals. For comparison, tag-based methods can only cover by a small percentage of animals in territory (Rowcliffe et al. 2014). None of the other terrestrial mammal investigation methods (track counts, fecal counts, questionnaire surveys, hunting statistics) could be applied in every ecosystem and for all species bigger than 1 kg weight (Akbaba and Ayas 2012). Camera traps have become a powerful and widely used tool in ecology and conservation. Gysel and Davis began exploring of camera traps as scientific tools in 1956 (Wearn and Glover-Kapfer 2017). In last decades the number of publications is rapidly increasing, from a few per year in 1995–2000 (Rovero et al. 2010) to almost 300 in 2016 (Wearn and Glover-Kapfer 2017). First of all, the camera traps have been used to big animals like bear (Zarzo-Arias 2019), big cat (Jackson et al. 2006, Karanth et al. 2006, Garrote et al. 2011, Cheyne et al. 2013) or ungulate (Rovero and Marshall 2009) monitoring. The tool was also used in the studies of medium size mammals like red fox (Sarmento et al. 2010, Diaz-Ruiz et al. 2015), pine marten (Manzo et al. 2011) and even for the small mammals (Bondi et al. 2010). Camera trap data were used to estimate species richness and site occupancy (Tobler et al. 2008, Rovero et al. 2010, Bowler et al. 2017, Hedwig et al. 2017), in the population ecology (Cheyne et al. 2013), for density estimation using capture-recapture sampling (Karanth et al. 2006, Garrote et al. 2011), and for analysis of the seasonal and daily activity (Ribout and Linkie 2009, Rowcliffe et al. 2014, Diaz-Ruiz et al. 2015, Caravaggi et al. 2018, Ogurtsov et al. 2018).

Seasonal and daily activity of free-living mammals is poorly known as it difficult to quantify activity in the field. There are few ways to study activity of mammals: direct visual observation, radio-collar or GPS telemetry (Ogurtsov et al. 2018). Different methods of testing animal activity give similar results to the camera method (Rovero and Marshall 2009, Bondi et al. 2010, Rowcliffe et al. 2014, Bowler et al. 2016, Lashley et al. 2018).

Therefore, we used camera traps as a tool to monitor mammals in the breeding colonies of great cormorants. The aim of our study was to find what species of mammals visit colonies and to analyse temporal patterns of their visits. We tested working hypothesis that cormorants are affecting seasonal and daily activity of all mammals. Such studies were not done before.

2. Material and methods

2.1 Study sites

2.1.1 The great cormorant colony in Juodkrantė

Great cormorant colony in Juodkrantė (further JCC) is located on the Curonian Spit, Kuršių Nerija National Park (WGS 55° 31' 13.82", 21° 6' 32.57", altitude 5–35 m) (Fig. 1). After 100 years of eradication, great cormorants (*Phalacrocorax carbo sinensis*) in JCC started to breed again in 1989. In 2015 the number of breeding pairs in this largest colony in Lithuania was estimated at about 3800 breeding pairs of great cormorants and 340 breeding pairs of grey herons (*Ardea cinerea*) (Knyva, unpublished). The colony is established in the mature pine forest. Most of the cormorant nests are twisted in pine, occasionally in spruce and oak. The area of the colony covers around 14 ha. The active part of the colony, with the highest concentration of nests and the strongest influence of birds, is characterized by scarce herb layer and dying or dead trees. Nitrophilic species of herbs dominate the herb layer, the projection of which is less than 10%. Oldest part of colony is already abandoned by cormorants. Trees in it are dead, many of them rotten, fallen and decaying. Trees and shrubs started re-growing, the herb layer is re-establishing. Among re-growth deciduous trees (*Quercus robur, Betula pubescens, Alnus glutinosa*) dominate (Matulevičiūtė et al. 2018).

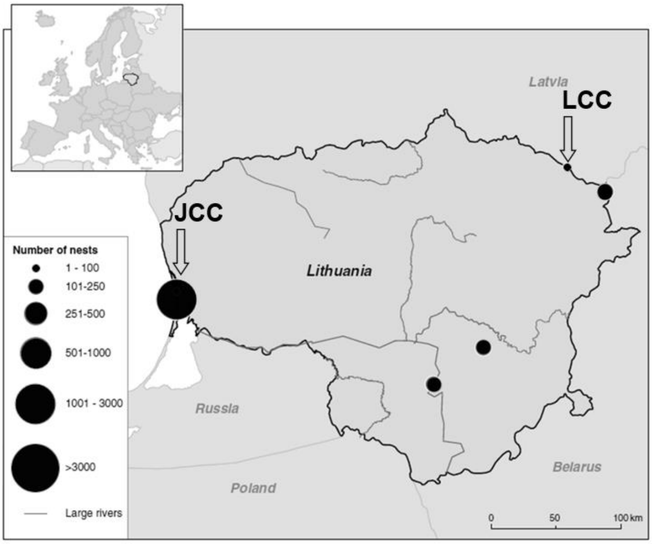

Fig. 1. Distribution and size of breeding colonies of the great cormorants (black circles) in Lithuania. Investigated sites marked by arrows: JCC – the great cormorant colony in Juodkrantė, LCC – the great cormorant colony in Lukštas Lake.

2.1.2 The great cormorant colony in Lukštas

Great cormorant colony in Lukštas Lake (further LCC) is located in East Lithuania, Zarasai district (WGS 55° 51' 0.41", 26° 12' 4.67", altitude 140 m) and situated in peninsula at the northern part of lake (Fig. 1). 130 breeding pairs were counted in 2016. Most nests are twisted in black alder, pine and birch trees. Grey herons are not present in the colony. The area of the colony covers around 1 ha.

2.2 Camera trapping

The activities of mammals were evaluated using camera traps (system with a motion trigger/sensor that activates a camera to take a photograph when an animal is present). We deployed camera traps in three points (one camera per point) in the JCC and one point in LCC.

Camera trapping in JCC lasted from November 2014 to September 2015 and from June 2017 to October 2018 involving 1376 trap days of effort. Camera trapping in LCC lasted from February 2015 to February 2016 and from November 2016 to July 2019 involving 1317 trap days of effort (Table S1).

In this study we used Ltl Acorn-5210A cameras. Sensors were set to the maximum sensitivity. The trigger interval was set at 0 sec. We used trail–targeted (passive camera) trapping design with no attractants. Cameras were mounted on the trees 40–60 cm above ground and checked (replacing batteries and SD memory cards) 3–4 times during the year. Time and date were automatically recorded on each picture. Pictures taken with at least 1–hour interval were treated as independent observations (trap events). Camera day lasted from 00:00 to 23:59. Year was divided into periods of the cormorant breeding time (BT) and non-breeding time (NT). BT lasted from April (when chicks begin to hatch from eggs) to July (when chicks finally leave the cormorant area). Non-breeding time was the period from August to March.

Each day was divided into three periods: daytime, nighttime and twilight. Twilight (T) was defined as a 60 minutes period before and after sunrise/sunset, so that each day had four twilight hours. Daytime (D) was a period between 60 minutes after sunrise and 60 minutes before sunset. Night (N) was a period between 60 minutes after sunset and 60 minutes before sunrise. Time of sunset and sunrise were estimated using the website www.day.lt.

Some devices failed to record time; for this reason we lost information about day activity in 117 trap events from JCC.

2.3 Diversity assessment and statistical analysis

In this study we used data on relative animal registrations independently of the fact that individuals may be registered several times in the same colony. Relative shooting frequency (RSF, photos/100 days) was calculated by formula: $RSF = (TE / TD) * 100$, where TE (trap events) = number of independent photographs; TD (effort of trapping days) = number of camera trapping days. For average values, SE, and 95% confidence interval (further – CI) were used. This way we override possible bias in registering the same animals several times or by different cameras.

Significance of differences was evaluated using ANOVA, pairwise comparisons according Student's t. Daily activity patterns were compared using chi–square statistics. Theoretical expected activity patterns were calculated based on the length of time of day periods in BT and NT. The minimum significance level was set at $p<0.05$. We used STATISTICA 6.0 (StatSoft 2004) for Windows. Mammal diversity in the cormorant colonies was evaluated using Shannon's diversity index H ($\log_2$ base), according to (Krebs 1999).

3. Results

3.1 Diversity of mammals in the great cormorant colonies

During 1317 trap days 668 independent photographs (trap events) were taken and 9 species of mammals were detected in LCC: red fox (*Vulpes vulpes*), raccoon dog (*Nyctereutes procyonoides*), roe deer (*Capreolus capreolus*), moose (*Alces alces*), wild boar (*Sus scrofa*), hare

(*Lepus* sp.), red squirrel (*Sciurus vulgaris*), marten (*Martes* sp.) and European badger (*Meles meles*). In JCC 895 independent photographs were taken during 1376 trap days and 9 species of mammals were registered: *S. scrofa*, *C. capreolus*, *A. alces*, *V. vulpes, N. procyonoides*, *S. vulgaris*, *Lepus* sp., raccoon (*Procyon lotor*), and sika deer (*Cervus nippon*) (Table 1, Fig. 2). Last three species are non-native to Lithuania. Shannon's diversity index in LCC and JCC were similar (Table 2).

Table 1. Relative shooting frequency (photos/100 days) and diversity indexes in the great cormorant colonies in Lukštas Lake (LCC) and Juodkrantė (JCC).

Species	**LCC, mean±SE (CI 95%)**	**JCC, mean±SE (CI 95%)**
A. alces	0.08±0.08 (0.19–0.47)	8.14±2.76 (6.77–16.23)
C. capreolus	7.82±1.77 (4.35–10.44)	23.18±2.37 (5.83–13.96)
C. nippon	–	1.16±0.82 (2.01–4.82)
S. scrofa	4.40±1.33 (3.27–7.84)	25.94±13.30 (32.64–78.23)
V. vulpes	18.60±6.50 (15.95–38.22)	4.94±1.03 (2.54–6.08)
N. procyonoides	18.53±8.95 (21.96–52.64)	0.29±0.15 (0.38–0.91)
P. lotor	–	0.51±0.43 (1.06–2.53)
Lepus sp.	0.84±0.45 (1.11–2.67)	0.15±0.09 (0.22–0.53)
S. vulgaris	0.15±0.14 (0.34–0.82)	0.73±0.23 (0.55–1.33)
Martes sp.	0.46±0.15 (0.36–0.86)	–
M. meles	0.08±0.07 (0.16–0.40)	–
Shannon's H	1.99	2.00

Table 2. Frequency of trap events (%) of *S. scrofa*, *V. vulpes* and *N. procyonoides* at the great cormorant colonies in Lukštas Lake (LCC) and Juodkrantė (JCC) throughout periods of the day in cormorant breeding time (BT) and non-breeding time (NT). T – Twilight, D – Daytime, N – Night.

Season	**Time**	**LCC**			**JCC**		
		S. scrofa	***V. vulpes***	***N. procyonoides***	***S. scrofa***	***V. vulpes***	***N. procyonoides***
BT	**N**	22.6	22.8	19.2	37	16.7	–
	T	16.1	18.0	22.7	39.1	33.3	–
	D	61.3	59.2	58.1	23.9	50.0	–
NT	**N**	100	30.8	70.0	25.4	28.6	100
	T	0	23.1	10.0	28.5	9.5	–
	D	0	46.2	20.0	46.1	61.9	–

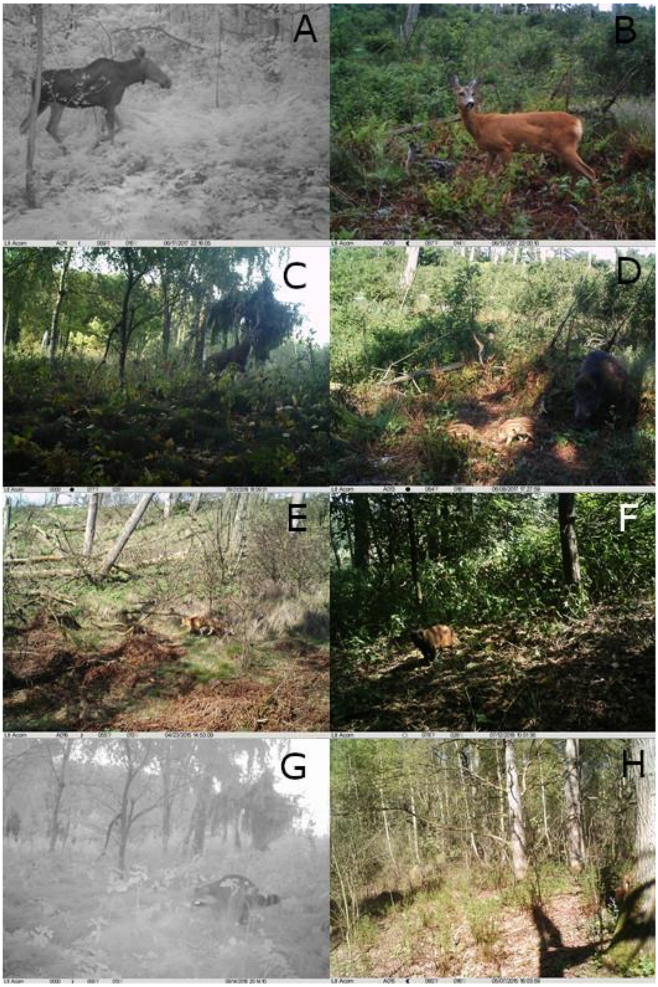

Fig. 2. Mammals registered by camera traps in great cormorants colonies (**A**: *A. alces*; **B**: *C. capreolus*; **C**: *C. nippon*; **D**: *S. scrofa*; **E**: *V. vulpes*; **F**: *N. procyonoides*; **G**: *P. lotor*; **H**: *S. vulgaris*).

3.2 Seasonal activity of mammals in cormorant colonies

Seasonal activity of mammals in LCC was dependent on breeding season (ANOVA F=29.7, p<0.001), in JCC differences between seasons were not found (F=0.21, p=0.65). The RSF differences were significant between species in both LCC (F=11.1, p<0.01) and JCC (F=2.6, p<0.05).

Moose in LCC was registered only once in February (Table S2). JCC in wintertime was not attractive for moose, however, from April onwards, moose registration frequencies increased with the peak of activity in August (28.3 photos/100 days) (Table S3).

Roe deer registration frequencies did not differ between seasons in both cormorant colonies. In LCC roe deer RSF was 6.2±2.5 (CI 2.83–18.62) photos/100 days in BT and 8.7±2.4 (CI 4.46–13.72) photos/100 days in NT (t=0.76, p=0.47), while in JCC respective values were 21.5±4.7 (CI 5.37–35.32) and 19.6±2.8 (CI 5.14–15.82) photos/100 days (t=0.87, p=0.41).

Wild boars visited LCC mainly in July, 12.7 photos/100 days and December, 12.9 photos/100 days (average – 2.5 photos/100 days in other months). RSF of wild boar in BT was 6.7±2.1 (CI 2.44–16.02) and 3.2±1.6 (CI 2.92–8.99) photos/100 days in NT (t=1.40, p=0.19) (Table S2; Fig. 3A). In JCC wild boars were most active in June, August and September: 21.0, 87.5 and 153.5 photos/100 days, respectively, while average RSF was 7.1 photos/100 days in other months (Table S3; Fig. 3B). In JCC wild boar relative shooting frequency in BT was 9.9±3.9 (CI 4.45–29.27), and in NT 34.8±19.5 (CI 36.44–112.17) photos/100 days. Though difference of RSF not significant (t=0.94, p=0.37), confidence intervals were not overlapping.

Red fox RSF in LCC was high from April (40.0 photos/100 days) to August (23.7 photos/100 days) with peak of activity in July (75.5 photos/100 days) (Table S2; Fig. 3A). Average ref fox RSF in BT was 41.8±11.1 (CI 12.60–82.92) photos/100 days compared to 5.9±2.7 (CI 5.11–15.75) photos/100 days in NT (t=4.39, p<0.05). Highest red fox RSF in JCC was in June, 13.8 photos/100 days, compared to 3.8 photos/100 days in other months (Table S3; Fig. 3B). Differences due to breeding were also significant, 6.2±2.3 (CI 2.65–17.47) photos/100 days in BT, compared to 2.9±0.7 (CI 1.29–3.96) in NT (t=2.31, p<0.05).

In LCC raccoon dog RSF was highest in breeding time, April (9.2 photos/100 days) to July (50.0 photos/100 days) with peak of activity in June (100.0 photos/100 days) (Table S2; Fig. 3A). Average raccoon dog RSF in BT was 50.0±18.8 (CI 21.31–140.27) photos/100 days, but just 1.3±1.4 (CI 0.87–2.68) photos/100 days in NT (t=3.74, p<0.05). In JCC raccoon dogs were photographed only 4 times (Table S3; Fig. 3B).

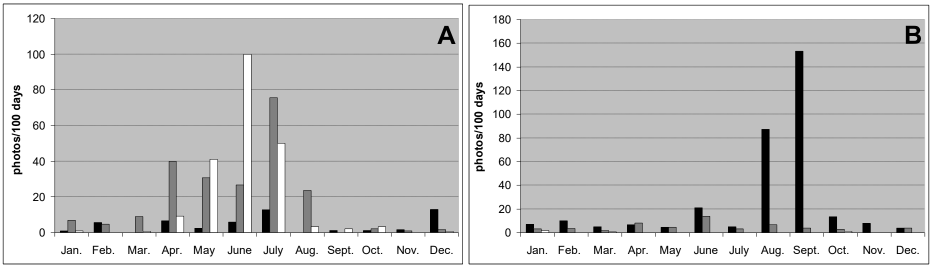

Fig. 3. Seasonal activity of *S. scrofa* (black column), *V. vulpes* (grey) and *N. procyonoides* (white) at great cormorant colonies in Lukštas Lake (LCC) and Juodkrantė (JCC).

3.3 Daily activity patterns of mammals

Without respect of the cormorant presence, moose (JCC χ^2=4.49, p=0.11), roe deer (LCC χ^2=8.7; JCC χ^2=7.19, p<0.05) and red fox (LCC χ^2=13.38, p<0.01; JCC χ^2=17.89, p<0.001) in both colonies were mostly active by day. Wild boar in LCC was mostly active by night (χ^2=12.68, p<0.01), and in JCC by day (χ^2=15.66, p<0.001). Raccoon dog in LCC was mostly active by day (χ^2=17.05, p<0.001; Table 2; df=2 in all cases above and below). Distribution of the hourly activities of mammals in LCC and JCC are given in Tables S3 and S4.

Breeding of the cormorants, however, brought radical changes in the daily activity patterns of most of the species (Table 2). In LCC wild boar during NT was active only at night (100%) (χ^2=31.9, p<0.001)). However, during the BT highest frequency of registrations of the wild boar was in the daytime (61.3% of all TE). Difference in the activity of wild boar between BT and NT was significant (χ^2=47.7, p<0.001).

In JCC activity peak of wild boar during NT was at daytime (46.1%) (χ^2=57.3, p<0.001). During BT activity switched to twilight (39.1%) and nighttime (37.0%) (χ^2=25.9, p<0.001; Table 2). Difference in the activity of wild boar between BT and NT was also significant (χ^2=42.1, p<0.001).

A similar trend was found in red fox activity in LCC, where daytime red fox activity was higher during BT (59.2%) than in NT (46.2%). Difference in activity patterns of red fox was significant between BT and NT (χ^2=6.1, p<0.05).

In JCC, on the contrary, daytime red fox activity was higher during NT (61.9% of all TE; χ^2=5.34, p=0.07) than in BT (50.0%; χ^2=7.43, p<0.05) (Table 2). Difference in activity patterns of red fox was significant between BT and NT (χ^2=20.0, p<0.001).

Raccoon dog daily activity peaks in LCC were also related to cormorant breeding time. In BT raccoon dog was active in daytime (58.1% of all TE) and this statistically significant from expected activity patterns, calculated by the time periods (χ^2=8.14, p<0.05). In NT raccoon dog activity peaks were registered at nighttime (70.0% of all TE; χ^2=2.35, p=0.31) (Table 2). In LCC raccoon dog activity patterns among BT and NT differed significantly (χ^2=45.2, p<0.001). In JCC, raccoon dog was registered in the nighttime only (Table 2).

4. Discussion

Following global development of the population of the great cormorants in the last decades, ecological impacts were investigated by many authors (Hobara et al. 2005, Goc et al. 2005, Gwiazda et al. 2010, Klimaszyk et al. 2015, Klimaszyk and Rzymsky 2016). Cormorants not only overload territory with nutrients and transform the environment. Part of fish brought to the colony as food for chicks is being lost (Pūtys 2012). Furthermore, during the cormorants breeding season, some chicks fall out of their nests. Lost fish and dropped chicks becoming easy prey for predator mammals. Changed environment affects nearly all aspects of the small mammals (Balčiauskienė et al. 2014, Balčiauskas et al. 2015), however changes in mammalian activity were not investigated. We present here first results of investigation of activity patterns of mammal in the colonies of great cormorants.

In the cormorant breeding season the intensity of the predator visits was greatly altered. We found, that in BT red fox visit frequency increased 2–7 times, compared to NT. In July, fox RSF was 75.5 photos/100 days, which is 12.5 times more frequent than in NT (see Table S2). In LCC, raccoon dog activity in BT increased 38.5 times (see Table S2, Fig. 3B).

Activity of the omnivorous wild boar was also affected by cormorants in JCC, visits to the area increased almost 3 times in BT (June), being, however, less intensive as in August and September, when wild boars were coming for acorns (see Table S3; Fig. 3B). In LCC with no oak trees, wild boar visits were over two times more frequent in BT (see Table S2; Fig. 3A).

Daily activity patterns in mammals are regulated by external factors such as food accessibility (Masi et al. 2009, Diaz Ruize et al. 2015). Cormorants feed their chicks in the daylight (Coleman and Richmond 2007), so it is time when they lose some of the prey. We found, that predators (foxes and raccoon dogs) and omnivores (wild boars) adapted to the cormorant activity during the day.

Other authors (Marques et al. 2018, Ogurtsov et al. 2018, Lee et al. 2019) pointed out that most mammals are mostly active at twilight and nighttime. Carnivore mammals are mainly characterised as nocturnal, as the nighttime is more successful time to find prey and avoid contact with people (Georgiev et al. 2015, Lee et al. 2019). Raccoon dog also exhibits nocturnal activity (Akbaba and Ayas 2012, Zoller and Drygala 2013, Ikeda et al. 2016). Ogurtsov et al. (2018) reported 64% trap events of raccoon dog at nighttime. Raccoon dog activity in NT was in agreement with these findings, as 85.7% of all TE in cormorant colonies were recorded in nighttime. However, availability of easy prey switched raccoon dogs to daytime activity: during BT 58.1% of registrations were in the daytime.

In England, Northern Ireland and Spain red foxes are categorized as a nocturnal (Doncaster and Macdonald 1997, Diaz-Ruiz et al. 2015, Caravaggi et al. 2018). In Turkey red fox was randomly active during the day and frequently active from 20:00 to 02:00 (Akbaba and Ayas 2012). Also, this predator categorized as a nocturnal in Bulgaria with a small activity peak in the daytime from 7:00 to 9:00 and from 12:00 to 14:00 (Georgiev et al. 2015). Servin et al. (1991) suggested that fox females are more active during the night than during the day then males are active during both day and night. However red fox has great behavioral plasticity in activity patterns which allows them to adapt to prey availability or other environmental changes (Diaz Ruize et al. 2015). In Japan red fox was categorized as a cathemeral (active throughout the day) animal (Ikeda et al. 2016).

Findings of our study support this view as in both investigated cormorant colonies fox was active in daytime (see Table 2). Differences were related to cormorant breeding season: in BT fox was more active at daytime in LCC (see Table 2). On the contrary, in JCC, fox was less active in daytime in BT compared to NT. We see here human–induced disturbance as a factor, influencing fox behavior. Curonian Spit, where JCC is situated, is one of the most visited territories in Lithuania. The cormorant colony is a popular tourist destination and has a viewing tower. At day, nearly all time tourists are present and disturbing foxes. On the contrary, LCC is difficult to access, so people do not visit it. Changes in animal activity patterns under human disturbance are confirmed by other authors (Doormal et al. 2015, Lee at al. 2019).

Wild boar activity is characterised as nocturnal (Caruso et al. 2018, Ogurtsov et al. 2018). In the cormorant colonies activity changes were observed: in LCC wild boar was more active at daytime (61.3% of all TE) in BT, while in NT at nighttime (see Tables 2, S4). In JCC activity patterns of wild boar were additionally influenced by human disturbance. In BT, when many visitors are registered, wild boar was active at nighttime and at twilight. In NT, when the number of visitors is minimal, wild boar was active at daytime (see Tables 2, S5).

Thus, colonies of great cormorants were influencing seasonal and daily activity of mammals, mostly predators (raccoon dog and red fox) and omnivorous wild boar. These behavioral changes make it possible to replenish foods with lost fish and nesting cormorant juveniles. Cormorant activity did not affect roe deer activity in both investigated colonies. In conclusion:

- Breeding activity of cormorants is most likely to alter the daily activity of raccoon dog, red fox, wild boar.
- In LCC average relative shooting frequency of these carnivores in the breeding season was a few times higher than in non-breeding time.
- In JCC average relative shooting frequency of red fox in BT was 2 times higher than in NT.

References

Adamonytė, G., R. Iršėnaitė, J. Motiejūnaitė, R. Taraškevičius and D. Matulevičiūtė. 2012. Myxomycetes in a forest affected by great cormorant colony: a case study in Western Lithuania. Fungal Divers. 13: 131–146.

Akbaba, B. and Z. Ayas. 2012. Camera trap study on inventory and daily activity patterns of large mammals in a mixed forest in north-western Turkey. Mammalia 76: 43–48.

Anderson, W.B. and G.A. Polis, 1999. Nutrient fluxes from water to land: seabirds affect plant nutrient status on Gulf of California islands. Oecologia 118: 324–332.

Balčiauskas, L., L. Balčiauskienė and M. Jasiulionis. 2015. Mammals under a colony of great cormorants: population structure and body condition of yellow-necked mice. Turk. J. Zool. 39: 941–948.

Balčiauskas, L., R. Skipitytė, M. Jasiulionis, G. Trakimas, L. Balčiauskienė and V. Remeikis. 2016. The impact of Great Cormorants on biogenic pollution of land ecosystems: Stable isotope signatures in small mammals. Sci. Total Environ. 565: 376–383.

Balčiauskas, L., R. Skipitytė, M. Jasiulionis, L. Balčiauskienė and V. Remeikis. 2018. Immediate increase in isotopic enrichment in small mammals following the expansion of a great cormorant colony. Biogeosciences 15: 3883–3891.

Balčiauskienė, L., M. Jasiulionis and L. Balčiauskas. 2014. Loss of diversity in a small mammal community in a habitat influenced by a colony of great cormorants. Acta Zool. Bulgar. 66: 229–234.

Balčiauskienė, L., L. Balčiauskas and M. Jasiulionis. 2015. Skull variability of mice and voles inhabiting the territory of a great cormorant colony. Biologia 70: 1406–1414.

Bondi, N., J.G. White, M. Stevens and R. Cooke. 2010. A comparison of the effectiveness of camera trapping and live trapping for sampling terrestrial small-mammal communities. Wildlife Res. 37: 456–465.

Bowler, M.T., M.W. Tobler, B.A. Endress, M.P. Gilmore and M.J. Anderson. 2017. Estimating mammalian species richness and occupancy in tropical forest canopies with arboreal camera traps. Remote Sens. Environ. 3: 146–157.

Caravaggi, A., M. Gatta, M.C. Vallely, K. Hogg, M. Freeman, E. Fadaei, J.T.A. Dick, W.I. Montgomery, N. Reid and D.G. Tosh. 2018. Seasonal and predator-prey effects on circadian activity of free-ranging mammals revealed by camera traps. PeerJ 6, e5827.

Caruso, N., A.E.J. Valenzuela, C.L. Burdett, V.E.M. Luengos, D. Birochio and E.B. Casanave. 2018. Summer habitat use and activity patterns of wild boar *Sus scrofa* in rangelands of central Argentina. PLoS ONE 13: e0206513.

Cheyne, S.M., D.J. Stark, S.H. Limin and D.W. Macdonald. 2013. First estimates of population ecology and threats to Sunda clouded leopards *Neofelis diardi* in a peat-swamp forest, Indonesia. Endanger. species res. 22: 1–9.

Coleman, J.T.H. and M.E. Richmond. 2007. Daily Foraging Patterns of Adult Double-Crested Cormorants during the Breeding Season. Waterbirds 30: 189–198.

Diaz-Ruiz, F., J. Caro, M. Delibes-Mateos, B. Arroyo, and P. Ferreras. 2015. Drivers of red fox (*Vulpes vulpes*) daily activity: prey availability, human disturbance or habitat structure? J. Zool. 298: 128–138.

Doncaster, C.P. and D.W. Macdonald. 1997. Activity patterns and interactions of red foxes (*Vulpes vulpes*) in Oxford city. Zool. Soc. London. 241: 73–87.

Doormaal, N., H. Ohashi, S. Koike and K. Kaji. 2015. Influence of human activities on the activity patterns of Japanese sika deer (*Cervus nippon*) and wild boar (*Sus scrofa*) in Central Japan. Eur. J. Wildlife Res. 61: 517–527.

Garcia, L.V., C. Ramo, C. Aponte, A. Moreno, M.T. Domínguez, L. Gómez-Aparicio, R. Redondo and T. Marañón. 2011. Protected wading bird species threaten relict centenarian cork oaks in a Mediterranean biosphere reserve: a conservation management conflict. Biol. Conserv. 144: 764–771.

Garrote, G., R.P. Ayala, P. Pereira, F. Robles, N. Guzman, F.J. García, M.C. Iglesias, J.Hervás, I. Fajardo and M. Simón. 2010. Estimation of the Iberian lynx population in the Doñana area, SW Spain, using capture-recapture analysis of camera-trapping data. Eur. J. Wildlife Res. 57: 355–362.

Georgiev, D., A. Mechev, E. Stoeva, G. Dilovski and A. Pavlova. 2015. On the activity of two medium-sized canids: the Golden Jackal (*Canis aureus*) and the Red Fox (*Vulpes vulpes*) in the Natural Bark “Sinite Kamani” (Bulgaria) revealed by camera traps. ZooNotes 69: 1–4.

Goc, M., L. Iliszko and L. Stempniewicz. 2005. The largest European colony of great cormorant on the vistula spit (N Poland) an impact of the forest ecosystem. Ecol. Quest. 6: 93–103.

Gwiazda, R., K. Jarocha and E. Szarek-Gwiazda. 2010. Impact of small cormorant (*Phalacrocorax carbo sinensis*) roost on nutrients and phytoplankton assemblages in the littoral regions of submontane reservoir. Biologia 65: 742–748.

Hedwig, D., I. Kienast, M. Bonnet, B.K. Curran, A. Courage, C. Boesch, H.S. Kuhl and T. King. 2017. A camera trap assessment of the forest mammal community within the transitional savannah-forest mosaic of the Bateke Plateau National Park, Gabon. Afr. J. Ecology 56 (4): 777–790.

Hobara, S., K. Koba, T. Osono, N. Tokuchi, A. Ishida and K. Kameda. 2005. Nitrogen and phosphorus enrichment and balance in forest colonized by cormorants: implications of the influence of soil adsorption. Plant Soil 268: 89–101.

Ikeda, T., K. Uchida, Y. Matsuura, H. Takahashi, T. Yoshida, K. Kaji and I. Koizumi. 2016. Seasonal and Diel Activity Patterns of Eight Sympatric Mammals in Northern Japan Revealed by an Intensive Camera-Trap Survey. PLoS ONE 11: e0163602.

Jackson, R.M., J.D. Roe, R. Wangchuk and D. Hunter. 2006. Estimating snow leopard population abundance using photography and capture-recapture techniques. Wildl. Soc. Bull. 34: 772–781.

Jasiulionis, M., L. Balčiauskas, L. Balčiauskienė and R. Taraškevičius. 2018. Accumulation of chemical elements in yellow-necked mice under a colony of great cormorants. Chemosphere 213: 156–163.

Kameda, K., K. Koba, S. Hobara, T. Osono and M. Terai. 2006. Pattern of natural 15N abundance in lakeside forest ecosystem affected by cormorant–derived nitrogen. Hydrobiologia 567: 69–86.

Karanth, K.U., J.D. Nichols, N.S. Kumar and J.E. Hines. 2006. Assessing tiger population dynamics using photographic capture-recapture sampling. Ecology 87: 2925–2937.

Klimaszyk P., and P. Rzymsky. 2016. The complexity of ecological impacts by great cormorants. Hydrobiologia 771: 13–30.

Klimaszyk, P., A. Brzeg, P. Rzymski and R. Piotrowicz. 2015. Black spots for aquatic and terrestrial ecosystems: impact of a perennial cormorant colony on the environment. Sci. Total Environ. 517, 222–231.

Kohno, H. and H. Ota. 1991. Reptiles in a seabird colony: herpetofauna of Nakanokamiishima Island of the yaeyama group, Ryukyu Archipelago. Island Studies in Okinawa 9: 73–89.

Krebs, C.J. 1999. Ecological methodology, 2nd ed. Menlo Park, CA: Addison-Welsey Educational Publishers, Inc.

Kutorga, E., R. Iršėnaitė, T. Iznova, J. Kasparavičius, S. Markovskaja and J. Motiejūnaitė. 2013. Species diversity and composition of fungal communities in a Scots pine forest affected by the great cormorant colony. Acta Mycologica 48: 173–188.

Lashley, M.A., M.V. Cove, M.C. Chitwood, G. Penido, B. Gardner, C.S. DePerno and C.E. Moorman. 2018. Estimating wildlife activity curves: comparison of methods and sample size. Sci. Rep-UK: 41–73.

Lee, H.J., J.W. Ha, S.J. Park, W.Y. Kim, J.Y. Cha, J.Y. Park, S.S. Choi, C.U. Chung and H.S. Oh. 2019. A study on the analysis of mammals' activity patterns and the effect of human hiker interference using camera trapping. J. Asia-Pac. Biodivers. 12: 57–62.

Manzo, E., P. Bartolommei, J.M. Rowcliffe and R. Cozzolino. 2012. Estimation of population density of European pine marten in central Italy using camera trapping. Acta Theriol. 57: 165–172.

Marques, R.V. and M.A. Fabian. 2019. Daily activity patterns of medium and large neotropical mammals during different seasons in an area of high altitude Atlantic rain forest in the South of Brazil. Rev Bras Zoo. 19: 38–64.

Masi, S., C. Cipolletta and M. Robbins. 2009. Western Lowland Gorillas (*Gorilla gorilla gorilla*) Change Their Activity Patterns in Response to Frugivory. Am. J. Primatol. 71: 91–100.

Matulevičiūtė, D., J. Motiejūnaitė, D. Uogintas, R. Taraškevičius, M. Dagys and V. Rašomavičius. 2018. Decline of a protected coastal pine forest under impact of a colony of great cormorants and the rate of vegetation change under ornithogenic influence. Silva Fenn. 52: 1–19.

Ogurtsov, S.S., A.S. Zheltukhin, and I.P. Kotlov. 2018. Daily activity patterns of large and medium-sized mammals based on camera traps data in the central forest nature reserve, Valdai upland, Russia. Nat. Conserv. Res. 3: 68–88.

Polis, G.A. and S.D. Hurd. 1996. Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. Am. Nat. 147: 396–423.

Pūtys, Ž. 2012. Great Cormorant *Phalacrocorax carbo Sinensis* Diet and its Effect on Fish Community in the Eutrophic Curonian Lagoon Ecosystem. Summary of doctoral dissertation. VUL, Vilnius: 1–48.

Ribout, M.S. and M. Linkie. 2009. Estimating overlap of daily activity patterns from camera trap data. J. Agric. Biol. Envir. S. 14: 322–337.

Rovero, F. and A.R. Marshall. 2009. Camera trapping photographic rate as an index of density in forest ungulates. J. Appl. Ecol. 46: 1011–1017.

Rovero, F., M. Tobler and J. Sanderson. 2010. Camera trapping for inventorying terrestrial vertebrates. In: J. Eymann, J. Degreef, C. Häuser, J. Monje, Y. Samyn, D.V. Spiegel (Eds.): Manual on Field Recording Techniques and Protocols for All Taxa Biodiversity Inventories. Brussels: Belgian National Focal Point to the Global Taxonomy Initiative: 100–128.

Rowcliffe, J.M., R. Kays, B. Kranstauber, C. Carbone and P.A. Jansen. 2014. Quantifying levels of animal activity using camera trap data. Methods Ecol. Evol. 5: 1170–1179.

Sarmento, P., J. Cruz, C. Eira and C. Fonseca. 2009. Evaluation of camera trapping for estimating red fox abundance. J. Wild. Manage. 73: 1207–1212.

Servin, J., J.R. Reu, and M. Delibes. 1991. Activity patterns of the red fox Vulpes vulpes in Donana, SW spain. Acta Theriol. 36: 369–373.

Silveira, L., A.T.A. Jacomo and J.A.F. Diniz-Filho. 2003. Camera trap, line transect census and track surveys: a comparative evaluation. Biol. Conserv. 114: 351–355.

Tobler, E.W., S.E. Carrillo-Percastegui, R.L. Pitman, R. Mares and G. Powell. 2008. An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals. Anim. Conserv. 11: 169–178.

Wearn, O.R. and P. Glover-Kapfer. 2019. Snap happy: camera traps are an effective sampling tool when compared with alternative methods. R. Soc. open sci. 6: 181748.

Wearn, O.R. and P. Glover-Kapfer. 2017. Camera-traping for conservation: a guide to best-practices WWF Conservation Technology Series 1.

Zarzo-Arias, A., V. Penteriani, M.M. Delgado, P.P. Torre, R. Garcia-Gonzalez, M.C. Mateo-Sanchez, P.V. Garcia and F. Dalerum. 2019. Identifying potential areas of expansion for the endangered brown bear (*Ursus arctos*) population in the Cantabrian Mountains (NW Spain). PLoS ONE 14: 1–15.

Zolkos, K., M. Kukwa and R. Afranowicz-Cieślak. 2013. Changes in the epiphytic lichen biota in the Scots pine (*Pinus sylvestris*) stands affected by a colony of grey heron (*Ardea cinerea*): a case study from northern Poland. Lichenologist 45: 815–823.

Zoller, H., and F. Drygala. 2013. Activity patterns of the invasive raccoon dog (*Nyctereutes procyonoides*) in North East Germany. Folia Zool. 62: 290–296.

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