



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



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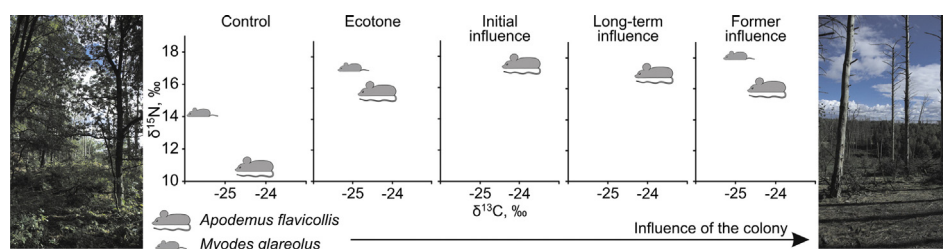
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### HIGHLIGHTS

- Cormorants transport nutrients from water to land ecosystems and pollute biogenically.
- We studied stable isotope composition of small mammal hair in 3 cormorant colonies.
- $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were measured using elemental analyzer–isotope ratio mass spectrometer.
- $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  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  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  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  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  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  $\delta^{15}\text{N}$  ( $16.31 \pm 3.01\%$  and  $17.86 \pm 2.76\%$ , respectively) were determined in those animals trapped in the biggest Great Cormorant colony.  $\delta^{15}\text{N}$  values were age dependent, highest in adult *A. flavicollis* and *M. glareolus* and lowest in juvenile animals. For  $\delta^{13}\text{C}$  values, age-dependent differences were not registered.  $\delta^{15}\text{N}$  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; Klimaszuk 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 (Klimaszuk 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 ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ,  $\delta^{34}\text{S}$ ) 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 ( $\delta^{13}\text{C}$ ) and stable nitrogen ( $\delta^{15}\text{N}$ ) 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.

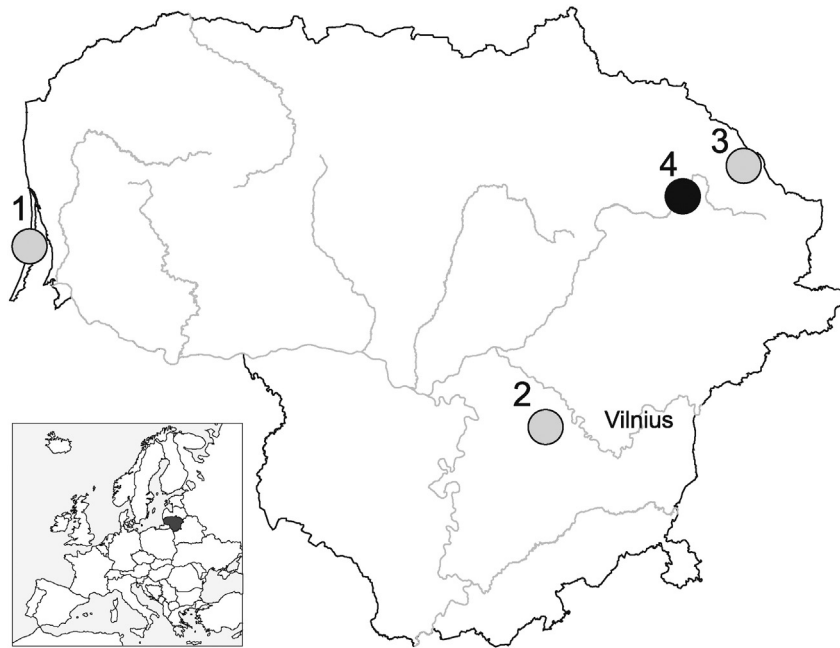


Fig. 1. Investigation sites in Lithuania. Great Cormorant colonies: 1 – Juodkrantė, 2 – Elektrėnai, 3 – Lukštas. Control site: 4 – Zarasai.

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  $\delta X$  values (where X represents the heavier isotope  $^{13}\text{C}$  or  $^{15}\text{N}$ ) or differences from given standards, expressed in parts per thousand (‰) and are calculated according to the formula:

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

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

Reference materials Caffeine IAEA-600 ( $\delta^{13}\text{C} = -27.771 \pm 0.043\text{‰}$ ,  $\delta^{15}\text{N} = 1 \pm 0.2\text{‰}$ ) and oil NBS-22 IAEA ( $\delta^{13}\text{C} = -30.031 \pm 0.043\text{‰}$ ) provided by the International Atomic Energy Agency (IAEA) were used as standards for calibration of the reference gases ( $\text{CO}_2$  and  $\text{N}_2$ ). EMA P2 (Elemental Microanalysis,  $\delta^{13}\text{C} = -28 \pm 0.1\text{‰}$ ,  $\delta^{15}\text{N} = -2 \pm 0.2\text{‰}$ ) was selected as a laboratory working standard. Repeated analysis of this reference material gave a standard deviation of  $<0.08\text{‰}$  for carbon and  $0.2\text{‰}$  for nitrogen.

## 2.4. Statistical analysis

To describe the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for all samples, the arithmetic mean  $\pm 1$  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  $\delta^{15}\text{N}$  was

influenced most significantly ( $r^2 = 0.77, F_{10,105} = 38.49$ ), that of  $\delta^{13}\text{C}$  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 ( $F_{10,101} = 0.76, \text{NS}$ ). Univariate tests for significance revealed dependence of  $\delta^{15}\text{N}$  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  $\delta^{13}\text{C}$  (Tukey HSD,  $p < 0.0001$ ),  $\delta^{15}\text{N}$  ( $p < 0.0002$ ), 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. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in *Apodemus flavicollis*

The distribution of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in *A. flavicollis* individuals showed significant variation (Fig. 2). The distribution of  $\delta^{15}\text{N}$  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  $\delta^{15}\text{N}$  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  $\delta^{15}\text{N}$  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.

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

The distribution of  $\delta^{13}\text{C}$  values in *A. flavicollis* showed no significant differences relating to animal age or gender. The average  $\delta^{13}\text{C}$  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. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in *Myodes glareolus*

In *M. glareolus*,  $\delta^{15}\text{N}$  values differed significantly between colonies and control territories ( $F_{3,65} = 10.36, p < 0.0001$ ). The highest  $\delta^{15}\text{N}$

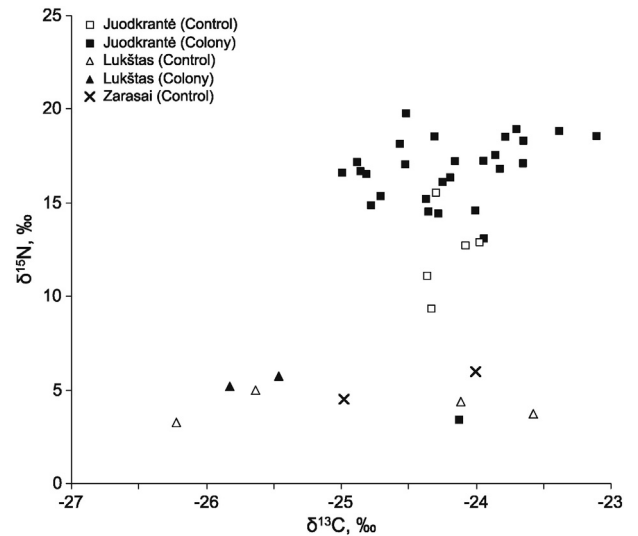


Fig. 2. Distribution of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in *A. flavicollis* hair from the colonies of Great Cormorants and control territories.

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  $p = 0.0001$ ).  $\delta^{15}\text{N}$  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  $\delta^{15}\text{N}$  values 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 ( $p = 0.06$ ).  $\delta^{15}\text{N}$  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  $\delta^{15}\text{N}$  in the hair of adult *M. glareolus* ( $11.72 \pm 1.07\%$ ) significantly exceeded those in young individuals ( $9.90 \pm 0.90\%$ , Tukey HSD,  $p < 0.05$ ).

$\delta^{13}\text{C}$  values in *M. glareolus* differed significantly between colonies and control territories ( $F_{3,65} = 3.81, p = 0.014$ ). The highest  $\delta^{13}\text{C}$  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  $\delta^{13}\text{C}$  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

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

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. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ 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  $\delta^{15}\text{N}$  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  $\delta^{15}\text{N}$  values (average  $10.98 \pm 0.99\%$ ) 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,  $\delta^{15}\text{N}$  values in the hair of *A. flavicollis* were higher than in the control zone: zone II (average  $\delta^{15}\text{N} = 17.58 \pm 0.93\%$ , Tukey HSD,  $p < 0.003$ ), zone III (average  $\delta^{15}\text{N} = 17.05 \pm 0.73\%$ ,  $p = 0.001$ ), zone IV (average  $\delta^{15}\text{N} = 16.14 \pm 1.37\%$ ,  $p = 0.001$ ) and zone V (average  $\delta^{15}\text{N} = 15.89 \pm 0.49\%$ ,  $p = 0.002$ ). Significant differences in  $\delta^{13}\text{C}$ , 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  $\delta^{15}\text{N}$  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  $\delta^{15}\text{N}$  values were registered in the hair of individuals trapped in the control zone (zone I, average  $14.30 \pm 3.02\%$ ), then higher in the ecotone ( $17.41 \pm 1.59\%$ ) and highest in zone IV ( $18.22 \pm 0.92\%$ ). 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).

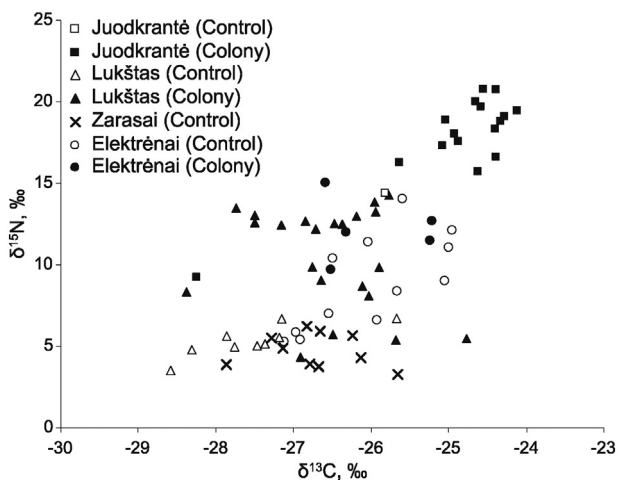


Fig. 3. Distribution  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in *M. glareolus* hair from the colonies of Great Cormorants and control territories.

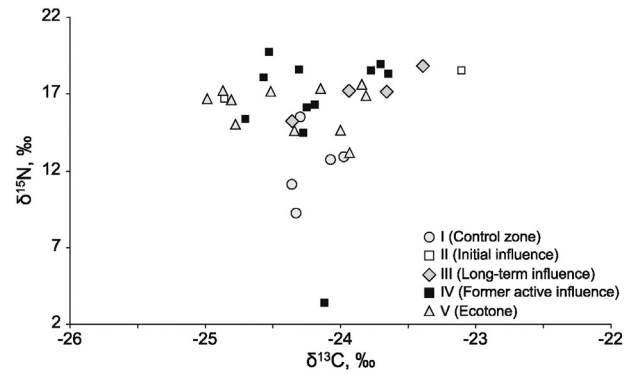


Fig. 4. Distribution  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in the hair of *A. flavicollis* trapped in the zones of Juodkrantė colony with different influence by Great Cormorants.

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).

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 permits 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  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  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  $\delta^{15}\text{N}$  values in *A. flavicollis* were dependent on the intensity and time of existence of the colony (Fig. 4). The  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  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  $\delta^{15}\text{N}$  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  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  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 $\delta^{13}\text{C}$ , ‰	±SD	Mean $\delta^{15}\text{N}$ , ‰	±SD
Benthic- 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	
<i>A. flavicollis</i> Juodkrantė (control)	−24.20	0.17	12.26	2.32
<i>A. flavicollis</i> Juodkrantė (colony)	−24.19	0.48	16.31	3.01
<i>A. flavicollis</i> Lukštas (control)	−24.89	1.25	4.06	0.71
<i>A. flavicollis</i> Lukštas (colony)	−25.64	0.27	5.46	0.37
<i>A. flavicollis</i> Zarasai (control)	−24.47	0.69	5.05	0.95
<i>M. glareolus</i> Juodkrantė (control)	−25.82		14.30	
<i>M. glareolus</i> Juodkrantė (colony)	−24.88	0.97	17.80	2.76
<i>M. glareolus</i> Lukštas (control)	−27.48	0.84	5.31	1.00
<i>M. glareolus</i> Lukštas (colony)	−26.54	0.80	10.46	3.14
<i>M. glareolus</i> Elektrėnai (control)	−26.02	0.79	8.86	2.91
<i>M. glareolus</i> Elektrėnai (colony)	−26.08	0.67	12.62	2.07
<i>M. glareolus</i> Zarasai (control)	−26.74	0.63	4.74	1.03

$16.0 \pm 1.9\%$  in the forest floor and  $16.4 \pm 4.5\%$  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  $3.4 \pm 1\%$  (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  $^{15}\text{N}$  and  $^{13}\text{C}$  (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  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  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 – its 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  $\delta^{15}\text{N}$  in their tissues (Nakagawa et al., 2007; Darling and Bayne, 2010). A positive correlation between  $\delta^{15}\text{N}$  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  $\delta^{15}\text{N}$  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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