

Article Association between Outlying Values in Body Condition Indices in Small Mammals and Their Habitats

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Abstract: Habitat type and habitat change are very important factors in the body condition of small mammals that inhabit them. The response can be positive, increasing, or the opposite, decreasing body condition. We analyzed outliers of the body condition indices (BCIs) of 12 species trapped in nine different habitats during 1980–2023 in Lithuania, a mid-latitude country. Mixed and fragmented habitats, as well as commensal habitats, could be considered the least suitable for small mammals, based on the highest proportions of underfit and low proportions of best-fit individuals. On the contrary, meadows and disturbed habitats (landfills and cormorant colonies) had the highest proportions of best-fit individuals, while the proportion of under-fit individuals was much lower than expected. We found outliers in the BCI in all species, except for the under-fit harvest mice (*Micromys minutus*), and in all habitats, though not numerous. The presence of the highest BCI in yellow-necked mice (*Apodemus flavicollis*) and bank voles (*Clethrionomys glareolus*) in the disturbed habitats studied and in house mice (*Mus musculus*) in commensal habitats may be related to the resources provided by these habitats. Our results demonstrate the feasibility of using retrospective small mammal morphometric data to analyze their relationship with habitat.

Keywords: body condition extremes; mice; voles; shrews; habitats; adaptation



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1. Introduction

Habitat is one of the most important factors determining the distribution and diversity of small mammal species and communities. On a global scale and over the last decades, the habitat factor operates in conjunction with climate change [1]. On a smaller scale, structural components of habitat influence the abundance of small mammals and the diversity of their communities [2]. The scale effect is important in defining habitat association with small mammals. On islands, habitat complexity increases the influence of interspecific competition on small mammals [3]. Coexistence in limited space requires a reduction in competition, leading to niche partitioning [4]. Habitat preferences of different small mammal species are not the same at patch and landscape scales [5], and, therefore, habitat preferences are scale-dependent [6]. As a result, different small mammal assemblages are associated with specific habitat types [7].

Two of the studies mentioned above really cover a wide range of material from both habitat and species perspectives [5,7]. However, these two studies do not address the fitness of small mammals, unlike our study of the relationship between body condition index (BCI) and habitat [8].

Research on the diversity and abundance of small mammals in Europe has focused on several habitat groups. Based on 35 years of data, M. Zárybnická et al. [9] found changes in small mammal populations based on landscape heterogeneity and forest management practices. The stability of small mammal communities was maintained by diverse habitats and influenced by both local biotic and abiotic factors. Forest habitats in Central Europe are the best studied as habitats supporting small mammals in terms of management practices, such as clear-cutting [10–12].

Farmland habitats have been the focus of small mammal studies due to conflicts over crop damage and food security [13,14] and the global conflict between agriculture and biodiversity conservation [15]. Some small mammal species, such as the greater white-toothed shrew (*Crocidura russula*) and the wood mouse (*Apodemus sylvaticus*), have been found to benefit from changes in agricultural land use, such as increases in grassland and fallow land [16]. These agri-environmental management practices are recommended by the EU. Fallow land and crops with long growing seasons provide cover for small mammals and the predators that prey on them, thus maintaining the diversity and abundance of their communities [17].

Knowledge of small mammal habitat associations can be translated into habitat management and restoration projects at local and landscape scales [18]. On a broader scale, studies of small mammals still do not provide a sufficient basis for their conservation strategies [19]. It should be noted, however, that none of the above studies assessed the fitness or body condition of small mammals, only their diversity and abundance. One of the most extensive studies, based on the analysis of owl prey, showed geographic variation in average prey weight, but this was not related to the body mass of specific individuals within a species or their body condition [20].

Similarly, most of the previous studies of small mammals and their habitats in Lithuania and other Baltic countries focused on their diversity and abundance [21–24]. Coastal wetlands, hemi-boreal forest-farmland landscapes, successional stages from grassland to forest, and commercial orchards were analyzed, but again, the biomass and not the mass of an individual was evaluated [25–28]. Thus, there are no publications that can be directly compared with our data, i.e., the extremal BCI values of various small mammal species and their distribution in habitats.

Undoubtedly, the link between habitat and body condition is through food resources and diet. We did not follow the general dietary classification presented in [29], but we analyzed BCIs of insectivores, omnivores, granivores, and herbivores. The relationship between small mammal diets and habitats has been analyzed in different habitats and at different latitudes [30–32], while in Lithuania, the focus was on commensal habitats [33], providing access to human-related foods. Our dietary studies, unfortunately, cover a much shorter period than the BCI study and are, therefore, not comparable without further research.

The Chitty effect, a common phenomenon in both the Americas and Europe, is related to the body condition of small mammals, as one of the manifestations of the effect is the presence of large-bodied individuals [34]. Changes in body mass are a common phenomenon in cyclic rodent populations [35], but the drivers of the Chitty effect are still incompletely understood. It is also not clear whether these large-bodied individuals have higher BCIs. Cyclicity in herbivores is one of the ecosystem functions [36]. Collapses in this function have been observed since the 1980s in different species and countries [37]. Regular cycles of abundance are being replaced by irregular fluctuations, sometimes leading to large-scale outbreaks [38].

Habitat has been reported as one of the factors modulating the abundance of largebodied common voles (*Microtus arvalis asturianus*) [35]. Larger individuals may have an advantage in resource use [39], but there is evidence that small individuals may also use a large proportion of resources [40,41].

Extra-large individuals of the field vole (*Microtus agrestis*) and sibling vole (*M. rossi-aemeridionalis*) were observed in agricultural habitats of Sweden [42], those of the root vole (*Alexandromys oeconomus*) in marshy habitats of Norway [43]. Large individuals in non-cyclic populations of common hamsters (*Cricetus cricetus*) were found in agricultural fields in the Czech Republic [44]. In North America, large individuals of Townsend's vole (*Microtus townsendii*) were recorded in grasslands [45], and those of meadow vole (*M. pennsylvanicus*) in old fields and former agricultural areas [46]. Information on the habitat distribution of extra small individuals is lacking.

The aim of this study was to analyze the habitat distribution of extreme (highest and lowest) values of the body condition index in different species of small mammals in Lithuania, representing mid-latitude countries with continental climates. We tested whether the distribution of these extreme values correlated with the proportions of individuals of each species caught in each habitat, i.e., whether the proportions of poorly and wellconditioned individuals were associated with specific habitats.

2. Materials and Methods

2.1. Study Site, Habitats, and Sample Size

Small mammals were trapped in Lithuania between 1980 and 2023, with 321 trapping sites covering the whole country (Figure 1). The choice of study sites and habitats has not been consistent, depending on research priorities at the time: in the 1970s, it was irrigated grasslands and protected areas with various habitats. In the 1980s, protected areas and their habitat complexes were further studied, and monitoring was conducted in the nuclear power plant region, focusing on forest, wetland, grassland, and agricultural habitats. In the 1990s, protected areas continued to be surveyed, and small mammals were captured in various areas and habitats in order to identify the most valuable sites in terms of biodiversity through complex surveys. National monitoring of small mammals was also carried out during this decade. In the 2000s, monitoring continued and a number of previously undesignated protected areas were surveyed. Specific studies were also undertaken to assess changes in small mammal communities in overgrowing meadows, to assess small mammal diversity on islands and small forest fragments in agroforestry, and to resurvey sites surveyed in the 1970s to compare results. Systematic surveys of small mammals in gardens, berry gardens, and commensal habitats began in the 2010s and continued into the 2020s. This choice of habitats and sites results in a random distribution across the country (Figure 1) and uneven trapping effort across habitats [47]. In the 1970s–1990s, surveys were mostly conducted during the growing season, but since the 2000s, they have also been conducted in winter.



Figure 1. Small mammal trapping sites in Lithuania, 1980–2023. Dot size corresponds to the number of analyzed individuals. Redrawn from [47].

For extreme body conditions, we analyzed 12 species with sample size N > 50. Based on the sample size, Mediterranean water shrew (*N. milleri*), hazel dormouse (*Muscardinus avellanarius*), northern birch mouse (*Sicista betulina*), wood mouse (*A. sylvaticus*), water vole (*Arvicola amphibius*), sibling vole (*M. rossiaemeridionalis*), Norway rat (*Rattus norvegicus*), and black rat (*R. rattus*) were excluded from analyses. The total sample size was 27,073 individuals. Two of the

analyzed trophic groups, omnivores and granivores, comprised more than 30% each, and two others were herbivores and insectivores, less than 20% each (Table 1).

| Species | Ν | % | Trophic Group | Ν | % |
|--|------|------|---------------|--------|------|
| Common shrew (Sorex araneus) | 2303 | 8.5 | | | |
| Pygmy shrew (S. minutus) | 724 | 2.7 | Insectivores | | |
| Water shrew (Neomys fodiens) | 99 | 0.4 | | 3126 | 11.5 |
| House mouse (<i>Mus musculus</i>) | 424 | 1.6 | o | | |
| Bank vole (Clethrionomys glareolus) | 9866 | 36.4 | Omnivores | 10,290 | 38.0 |
| Striped field mouse (<i>Apodemus agrarius</i>) | 3482 | 12.9 | | | |
| Yellow-necked mouse (A. flavicollis) | 5403 | 20.0 | • • • | | |
| Pygmy field mouse (A. uralensis) | 68 | 0.3 | Granivores | | |
| Harvest mouse (Micromys minutus) | 337 | 1.2 | | 9290 | 34.3 |
| Root vole (Alexandromys oeconomus) | 1286 | 4.8 | | | |
| Common vole (Microtus arvalis) * | 2429 | 9.0 | Herbivores | | |
| Short-tailed vole (M. agrestis) | 652 | 2.4 | | 4367 | 16.1 |

Table 1. Sample composition of small mammals used for this study.

*—Sensu lato. In most studies, the sibling vole, Microtus rossiaemeridionalis, was not specifically identified.

All habitats studied were categorized into nine groups (Table 2). Most small mammals were captured in meadows and forests, followed by commensal habitats, then wetlands, disturbed habitats (represented by landfills and breeding colonies of Great Cormorants situated in riparian or continental woodlands), and agricultural habitats. The representation of shrub and riparian habitats was about 2% or less, while 4.3% of all small mammals were trapped in fragmented habitats, which included a mix of wetlands, forests, meadows, and agricultural land. The trapping effort was also not even. However, mixed habitats included other categories, such as forests, meadows, and wetlands (Table 2).

Table 2. Habitat distribution of small mammal sample: TE—trapping effort, days; N—number of individuals; S—number of species; n, I—number of insectivores; %, I—proportion of insectivores; n, O—number of omnivores; %, O—proportion of omnivores; n, G—number of granivores; %, G—proportion of granivores; n, H—number of herbivores; %, H—proportion of herbivores.

| Habitat | TE | Ν | % | S | n, I | %, I | n, O | % , O | n, G | %, G | n, H | %, H |
|--------------|---------|--------|------|----|------|------|--------|--------------|------|------|------|------|
| Forest | 110,075 | 7195 | 26.6 | 12 | 463 | 6.4 | 4576 | 63.6 | 1948 | 27.1 | 208 | 2.9 |
| Shrub | 4200 | 349 | 1.3 | 11 | 86 | 24.6 | 120 | 34.4 | 117 | 33.5 | 26 | 7.4 |
| Wetland | 40,968 | 2161 | 8.0 | 12 | 412 | 19.1 | 1285 | 59.5 | 315 | 14.6 | 149 | 6.9 |
| Meadow | 119,700 | 7246 | 26.8 | 12 | 1325 | 18.3 | 877 | 12.1 | 3077 | 42.5 | 1967 | 27.1 |
| Riparian | 9069 | 600 | 2.2 | 9 | 71 | 11.8 | 171 | 28.5 | 226 | 37.7 | 132 | 22.0 |
| Mixed | 137,040 | 1163 | 4.3 | 12 | 187 | 16.1 | 490 | 42.1 | 322 | 27.7 | 164 | 14.1 |
| Disturbed | 19,525 | 1921 | 7.1 | 11 | 66 | 3.4 | 765 | 39.8 | 1054 | 54.9 | 36 | 1.9 |
| Agricultural | 24,638 | 2066 | 7.6 | 11 | 83 | 4.0 | 404 | 19.6 | 892 | 43.2 | 687 | 33.3 |
| Commensal | 26,516 | 4372 | 16.1 | 12 | 433 | 9.9 | 1602 | 36.6 | 1339 | 30.6 | 998 | 22.8 |
| Total | 491,731 | 27,073 | 100 | 12 | 3126 | 11.5 | 10,290 | 38.0 | 9290 | 34.3 | 4367 | 16.1 |

As shown in [9–13,15–19,25–28,30–32,43], there is no standard habitat classification used in small mammal trapping. The grouping used here is not based on CORINE, although it does include some Level 3 habitats [7]. In the commensal habitat group, we included industrial and commercial areas, farms, farmsteads, cattle barns, and individual houses. The agricultural habitat group included arable land, perennial and annual crops, and complex cropping patterns. Disturbed habitats included mines, landfills, and construction sites, according to CORINE [7], as well as sites with strong disturbance of biological origin and territories of breeding cormorant colonies. Apart from these, small mammals were only captured in closed landfills. The riparian habitat group included

meadows, wetlands, forests, and other habitats within 50 m from the shore of a river, lake, or island. This group has no equivalent in the CORINE classification. The meadows group included natural or seeded grasslands and pastures, including flooded meadows. Wetland habitats include all wetland habitats, from marshes to peat bogs; in the description of the trapping sites, the habitat in 70% of the cases was characterized as "wetland" only, and the presence of reed beds was indicated in ~7% of the trapping sites. Shrub habitats are defined as a transitional woodland–shrub in the CORINE classification [7]; both "shrub" and "shrub-covered meadow" account for 40% of the trap descriptions. Forest habitats include deciduous, coniferous, and mixed forests regardless of their age; characterizations of this habitat were the most variable, with over 100 different descriptions. Finally, mixed habitats also have no CORINE equivalent, and this category was chosen when a 125 m trap line covered several different habitats so that mixed habitats were also fragmented habitats. We expect that such a broad classification will ensure better compatibility with the results of other small mammal researchers.

2.2. Small Mammal Collection and Processing Methods

The capture of small mammals was conducted using the established snap-trapping methodology, employing trap lines comprising 25 traps spaced 5 m apart. Until they were transported to the laboratory and processed, the captured individuals were stored frozen. The identification of species was based on external features. *Microtus* voles were identified by their teeth. Trapped individuals were weighed to the nearest 0.1 g and their body length was measured to the nearest 0.1 mm using calipers. Further details on the trapping and processing of small mammals can be found in previous publications [8,47].

2.3. Data Analysis

The body condition index (BCI) was calculated according to the formula proposed by P.J. Moors: BCI = $(Q/L^3) \times 10^5$ [48]. In this equation, Q represents the body weight in grams (exclusive of the uterine weight with embryos for pregnant females), while L denotes the body length in millimeters.

The mean BCI for all small mammal species except rats in Lithuania is 3.03 (1.04–6.89) [47]. BCI statistics for all species analyzed are presented in Table S1 in the Supplement. To facilitate analysis, extreme values were set as BCI < 2.0 and BCI > 5.0, while individuals with BCI > 4.0 were considered to be in good condition. All analyzed small mammal species except *M. minutus* have BCI values < 2.0, and all except *N. fodiens* and *A. uralensis* have BCI values > 5.0.

The proportions of individuals exhibiting extreme BCI values were assessed across all habitats, and these were then compared with the expected proportions. The expected proportions were calculated on the assumption that they must correspond to the number of samples of individuals. The chi-square was calculated in PAST, version 4.13 (Museum of Paleontology, Oslo College, Oslo, Norway) [49], using the "sample vs. expected" routine with Monte Carlo permutation (N = 9999). The minimum confidence level was set at p < 0.05.

3. Results

3.1. Are All Habitats Equally Good?

The proportions of small mammals with extreme BCI values were not in accordance with the expected values (Table 3). These differences were found to be significant for BCI < 2 ($\chi^2 = 217.6$), BCI > 4 ($\chi^2 = 343.8$), and BCI > 5 ($\chi^2 = 62.1$) at *p* < 0.0001 with df = 8.

| 1 | BCI | Forest | Shrub | Wetland | Meadow | Riparian | Mixed | Disturbed | Agricultural | Commensal |
|-----|-------|--------|-------|---------|--------|----------|-------|-----------|--------------|-----------|
| | Obs n | 38 | 9 | 32 | 89 | 2 | 36 | 6 | 8 | 141 |
| -0 | Obs % | 10.5 | 2.5 | 8.9 | 24.7 | 0.6 | 10.0 | 1.7 | 2.2 | 39.1 |
| <2 | Exp n | 95.9 | 4.7 | 28.8 | 96.6 | 8.0 | 15.5 | 25.6 | 27.5 | 58.3 |
| | Exp % | 26.6 | 1.3 | 8.0 | 26.8 | 2.2 | 4.3 | 7.1 | 7.6 | 16.1 |
| | Obs n | 273 | 23 | 56 | 513 | 22 | 7 | 225 | 181 | 191 |
| × 4 | Obs % | 18.3 | 1.5 | 3.8 | 34.4 | 1.5 | 0.5 | 15.1 | 12.1 | 12.8 |
| >4 | Exp n | 396.3 | 19.2 | 119.0 | 399.1 | 33.0 | 64.1 | 105.8 | 113.8 | 240.8 |
| | Exp % | 26.6 | 1.3 | 8.0 | 26.8 | 2.2 | 4.3 | 7.1 | 7.6 | 16.2 |
| | Obs n | 22 | 1 | 2 | 66 | 5 | 0 | 22 | 5 | 17 |
| | Obs % | 15.7 | 0.7 | 1.4 | 47.1 | 3.6 | 0.0 | 15.7 | 3.6 | 12.1 |
| >5 | Exp n | 37.2 | 1.8 | 11.2 | 37.5 | 3.1 | 6.0 | 9.9 | 10.7 | 22.6 |
| | Exp % | 26.6 | 1.3 | 8.0 | 26.8 | 2.2 | 4.3 | 7.1 | 7.6 | 16.1 |

Table 3. The numbers and proportions of individuals with extreme BCI in habitats irrespective ofsmall mammal species. Obs: observed; Exp: expected.

Mixed and fragmented habitats can be regarded as the most problematic, as the proportion of under-fit small mammals was twice as high as expected. In addition, there were no over-fit individuals with BCI > 5, and the proportion of small mammals with BCI > 4 was nine times less than expected (Table 3). Similarly, a higher-than-expected proportion of small mammals with BCI < 2 and a lower-than-expected proportion of over-fit individuals were present in commensal habitats. These trends were less pronounced in wetlands.

Based on the analysis of BCI extremes, the investigated disturbed habitats and meadows can be characterized as the "best" ones. In disturbed habitats, the proportion of small mammals with BCI < 2 is four times less than what would be expected, while the proportion of individuals exhibiting the best fit is at least twice as large as what would be expected. A similar pattern, albeit less pronounced, is observed in meadows (Table 3).

3.2. Distribution of Species Extremes across Habitats

The observed and expected frequencies of individuals in various small mammal species with BCI < 2 were recorded in forests ($\chi^2 = 52.9$), wetlands ($\chi^2 = 78.2$), and meadows ($\chi^2 = 137.5$). Significant differences were observed between mixed ($\chi^2 = 157.4$), agricultural ($\chi^2 = 248.0$), and commensal ($\chi^2 = 519.0$) habitats (all p < 0.0001, df = 11). In shrub, riparian, and disturbed habitats, the observed proportions of underfit individuals in various small mammal species did not differ from those expected (Table A1).

Among individuals of different species with BCI < 2, the majority of *S. minutus*, *M. musculus*, *C. glareolus*, and *M. arvalis* were captured in commensal habitats, while the majority of *S. araneus*, *N. fodiens*, *A. agrarius*, *A. uralensis*, and *A. oeconomus* were captured in meadows (Figure 2a).

The influence of habitat was also discernible in the distribution of over-fit individuals with BCI > 4, with the exception of those captured in mixed habitats (Table A2).

Among individuals of different species with BCI > 4, the majority of *S. araneus*, *S. minutus*, *N. fodiens*, *A. agrarius*, *M. minutus*, *A. oeconomus*, and *M. agrestis* were captured in meadows, while the majority of *C. glareolus* and *A. flavicollis* were caught in forests. *M. musculus* was found in commensal habitats, and the majority of *M. arvalis* were captured in agricultural settings (Figure 2b).

The observed proportions of extremely overfit individuals with BCI > 5 significantly differed from expected proportions in forests ($\chi^2 = 62.6$, p < 0.0001, df = 11), meadows ($\chi^2 = 140.7$, p < 0.0001, df = 11), disturbed habitats ($\chi^2 = 37.1$, p < 0.001, df = 11), and commensal habitats ($\chi^2 = 47.6$, p < 0.0001, df = 11). In the shrub, wetland, riparian, mixed,



and agricultural habitats, the proportions of individuals with extremely high BCI were in accordance with the sample size of species (Table A3).

Figure 2. The frequency of occurrence of small mammal individuals with extreme BCI values in relation to habitat.

The habitat distribution of these individuals was nearly identical to that described above. The majority of *S. araneus, S. minutus, A. agrarius, M. minutus,* and *A. oeconomus* were captured in meadows, *A. flavicollis* in disturbed habitats, *C. glareolus* in forests, *M. musculus* in commensal habitats, and the majority of *M. arvalis* in agricultural habitats (Figure 2c).

3.3. Distribution of Body Condition Index Extremes in Small Mammal Species

The analysis revealed that when considering only individuals with BCI < 2, meadows, mixed, disturbed, agricultural, and commensal habitats are characterized by an over-representation of *S. minutus*. Conversely, forests were overrepresented by an under-fit *C. glareolus*, while shrub and wetland areas were overrepresented by *S. araneus* (Figure 3a).

The majority of forests and disturbed habitats were represented by two species: *A. flavicollis* and *C. glareolus*, with BCI > 4. In commensal habitats, BCI > 4 was best represented by *N. fodiens* and *A. flavicollis*, while in agricultural habitats, by *M. arvalis* and *A. agrarius*. In wetlands, *C. glareolus* with BCI > 4 was represented most frequently (Figure 3b).

The same two species, *A. flavicollis* and *C. glareolus*, were most prevalent among individuals with BCI > 5 in disturbed habitats, *M. musculus* in commensal habitats, *M. minutus* in meadows, and *A. flavicolis* in forests (Figure 3c).



Figure 3. Proportions of small mammal species with extreme BCI values observed in the investigated habitats.

4. Discussion

A review of the literature reveals that no study has previously compared the variability of individual fitness across different habitats and species. Our study, which examines the distribution of BCI thresholds across species and habitats, therefore, makes an original contribution to our understanding of the relationship between fitness and habitat.

Outlying values in body condition indices (BCI < 2 and BSI > 4) were observed in all investigated habitats and in all species, with the exception of *M. minutus*, which was never under-fit. At BCI values greater than 5, however, no small mammals were captured in mixed habitats, with only a few individuals observed in shrub, wetland, riparian, and agricultural habitats. These highest BCI values were not observed in *N. fodiens* and *A. uralensis*, and were observed in only a few individuals in *M. arvalis* and *M. agrestis*.

Thus far, other investigators have documented the presence of extra-large individuals in a range of habitats, including agricultural settings [42,44,46], grasslands [45], and wetlands [43]. However, there is a paucity of information regarding underfit individuals. The high number of *M. musculus* with BCI > 5 observed in commensal habitats can be attributed to the availability of rich food sources and species adaptations [50], as is the case for *M. minutus* in meadows (and also in riparian and agricultural habitats, as illustrated in Figure 3b,c) due to their scansorial lifestyle and preference for rich and protective habitats, such as reedbeds [51].

The presence of over-fit *A. flavicollis* and *C. glareolus* in disturbed habitats, such as landfills and colonies of great cormorants (*Phalacrocorax carbo*), is associated with elevated concentrations of nitrogen, phosphorus, carbon, and other biogens [52]. As a consequence of elevated nitrogen concentrations in the basal resources of small mammals, already evident in the first year of the cormorant colony's presence, there is a distortion of the trophic

level of these small mammals. For instance, the isotopic δ^{15} N signatures of granivorous *A. flavicollis* and omnivorous *C. glareolus* in the cormorant colony are higher than those of insectivores in other habitats [53]. Additionally, the concentration of biogenic elements originating from food waste and industrial discharges is elevated in landfills, resulting in environmental consequences [54].

Theoretically, several mechanisms can contribute to species-specific overfitness, including genetic, ecological, behavioral, and physiological factors, but again, so far, we have only analyzed individual fitness. What could be tested at the site level by other authors is ecological release (reduced competition in environments where the number of competing species is reduced, allowing them to increase in number and increase individual fitness. Such a situation might occur in newly colonized areas after a strong disturbance.

What is the role of BCI in the context of broader issues in species biology? Individuals of the same species exhibit variation in size and other characteristics, which is a prerequisite for natural selection to occur [55]. The impact of individual heterogeneity operates at multiple scales, from the individual to the species and ecosystem level [56]. However, there is still a dearth of knowledge regarding the large-scale investigation of co-occurring species in the same habitats within BCI. Improved body condition can serve as a buffer against adverse environmental conditions and changes, enhancing the likelihood of survival [57].

The impact of habitat on the body condition of small mammals has been documented, with habitat quality identified as the most crucial factor [58]. The body condition of these animals is found to be associated with habitat type [59], as well as with various forms of habitat alteration, including agricultural practices [60] and habitat loss [61]. Human activity can exert a detrimental (reducing activity and occurrence) or beneficial influence on small mammals, with more than half of the species demonstrating a positive response [62]. Therefore, the mechanism is not straightforward, and further insight into BCI and habitats is necessary. Commensal and non-commensal small mammal species may adapt to urban environments by modifying their behavior [63]. In our study, small mammal BCIs did not demonstrate adaptation to commensal habitats, with the exception of *M. musculus*, a typical synanthropic species.

The intra- and inter-species dietary differences may be attributed to both body size [64] and trophic group [65], with herbivores exhibiting the highest risk. In low-latitude regions, the decline of small mammals is likely to be most pronounced as a consequence of deforestation [66], which can be defined as the destruction of and the subsequent fragmentation of remaining patches. In Lithuania, the decline in meadows over the past three decades [8] may have been a significant factor, as this habitat supports a higher-than-expected population of small mammals with the best body condition.

Nevertheless, the capacity of small mammal species to adapt is not confined to urban environments [63]. It was demonstrated that Tullberg's soft-furred mouse (*Praomys tullbergi*) is capable of responding to fluctuations in resource availability by adjusting its individual body condition [67]. Consequently, an understanding of the adaptive strategies employed by different species in diverse habitats is crucial for the development of effective conservation strategies. As stated by J.W. Moore and D.E. Schindler, "Adaptation ultimately underpins the resilience of Earth's complex systems; species, communities, and ecosystems shift and evolve over time." [68]. This underscores the importance of long-term trends and baselines, as well as the utilization of body condition indicators that can be obtained retrospectively in other countries.

5. Conclusions

Based on long-term BCI variability, outliers in the body condition were present in all investigated species and habitats, with the exception of *M. minutus*, which exhibited no under-fit individuals.

The presence of the highest BCI levels can be attributed exclusively to habitat characteristics, particularly the resources provided in some cases: *A. flavicollis* and *C. glareolus* in disturbed habitats and *M. musculus* in commensal habitats. The relative proportions of under- and over-fit small mammals of different species indicate that mixed/fragmented and commensal habitats may be considered the least favorable, while meadows and disturbed habitats may be considered the most favorable.

Given the possibility of retrospective assessment of the BCI in question, the index may prove useful for investigating adaptations to human influence and climate change.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/land13081271/s1, Table S1: Body condition index statistics of small mammal species with N > 50, based on [47].

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Institutional Review Board Statement: The study uses historical material on small mammal trapping and material collected for other projects. It was conducted in accordance with the Lithuanian legislation (the Republic of Lithuania Law on the Welfare and Protection of Animals No. XI-2271, "Requirements for the Housing, Care and Use of Animals for Scientific and Educational Purposes", approved by Order No B1-866, 31 October 2012 of the Director of the State Food and Veterinary Service (Paragraph 4 of Article 16) and the European legislation (Directive 2010/63/EU) on the protection of animals, and was approved by the Animal Welfare Committee of the Nature Research Centre, protocols No GGT-7 and GGT-8).

Informed Consent Statement: Not applicable.

Data Availability Statement: This is an ongoing research. Therefore, data are available from the corresponding author upon request.

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Appendix A

Table A1. Observed and expected frequencies of individuals with BCI < 2 in different small mammal species depending on habitat. Green cells: observed frequencies \geq 3 times more than expected ones; brown cells: observed frequencies \geq 3 times less than expected ones; ***—*p* < 0.0001, NS—not significant.

| Species with | For | est | Shr | rub We | | and | and Meadow | | Riparian | | Mixed | | Disturbed | | Agricultural | | Commensal | |
|----------------|------|------|------|--------|--------------|------|------------|-------|----------|-----|-----------|------|-----------|-----|--------------|-----|-----------|------|
| BCI < 2 | Obs | Exp | Obs | Exp | Obs | Exp | Obs | Exp | Obs | Exp | Obs | Exp | Obs | Exp | Obs | Exp | Obs | Exp |
| S. araneus | 6 | 1.8 | 4 | 1.5 | 11 | 4.5 | 17 | 12.4 | 1 | 0.2 | 6 | 4.1 | 0 | 0.2 | 1 | 0.2 | 16 | 9.4 |
| S. minutus | 5 | 0.6 | 1 | 0.6 | 10 | 1.3 | 21 | 3.5 | 0 | 0.1 | 16 | 1.5 | 4 | 0.0 | 5 | 0.1 | 47 | 4.0 |
| N. fodiens | 0 | 0.1 | 0 | 0.0 | 0 | 0.3 | 2 | 0.3 | 0 | 0.0 | 0 | 0.3 | 0 | 0.0 | 0 | 0.0 | 0 | 0.5 |
| M.musculus | 0 | 0.0 | 0 | 0.0 | 0 | 0.1 | 0 | 0.2 | 0 | 0.0 | 0 | 0.1 | 0 | 0.0 | 0 | 0.1 | 1 | 11.7 |
| C. glareolus | 24 | 24.1 | 2 | 3.1 | 8 | 19.0 | 4 | 10.6 | 0 | 0.6 | 6 | 15.1 | 2 | 2.4 | 0 | 1.5 | 45 | 39.9 |
| A. agrarius | 0 | 0.7 | 0 | 0.9 | 1 | 1.5 | 7 | 26.0 | 0 | 0.2 | 0 | 3.1 | 0 | 0.3 | 0 | 1.4 | 0 | 14.7 |
| A. flavicollis | 2 | 9.4 | 0 | 2.0 | 1 | 2.7 | 1 | 8.7 | 0 | 0.5 | 1 | 6.5 | 0 | 2.9 | 1 | 2.0 | 1 | 27.7 |
| A. uralensis | 0 | 0.1 | 0 | 0.0 | 0 | 0.1 | 1 | 0.3 | 0 | 0.0 | 0 | 0.2 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| M. minutus | 0 | 0.1 | 0 | 0.1 | 0 | 0.3 | 0 | 2.8 | 0 | 0.0 | 0 | 0.2 | 0 | 0.0 | 0 | 0.1 | 0 | 0.7 |
| A. oeconomus | 1 | 0.2 | 0 | 0.2 | 1 | 0.5 | 19 | 11.8 | 0 | 0.3 | 1 | 0.8 | 0 | 0.0 | 0 | 0.3 | 1 | 1.2 |
| M. arvalis | 0 | 0.3 | 1 | 0.2 | 0 | 0.7 | 16 | 9.8 | 1 | 0.1 | 3 | 1.3 | 0 | 0.0 | 1 | 2.1 | 28 | 28.8 |
| M. agrestis | 0 | 0.5 | 1 | 0.2 | 0 | 1.0 | 1 | 2.6 | 0 | 0.1 | 3 | 3.0 | 0 | 0.1 | 0 | 0.2 | 2 | 2.2 |
| Total | 38 | 38 | 9 | 9 | 32 | 32 | 89 | 89 | 2 | 2 | 36 | 36 | 6 | 6 | 8 | 8 | 141 | 141 |
| χ^2 | 52.9 | *** | 14.4 | NS | 78.2 *** 137 | | 137.5 | 5 *** | 13.1 | NS | 157.4 *** | | 3.6 NS | | 248 *** | | 519 *** | |

| Species with | Forest | | Shrub | | Wetland | | Mea | Meadow | | Riparian | | Mixed | | rbed | Agricultural | | Commensal | |
|----------------|-----------|-------|-------|-----|----------|------|-----------|--------|--------|----------|--------|-------|--------|-------|--------------|------|-----------|------|
| BCI > 4 | Obs | Exp | Obs | Exp | Obs | Exp | Obs | Exp | Obs | Exp | Obs | Exp | Obs | Exp | Obs | Exp | Obs | Exp |
| S. araneus | 18 | 12.7 | 2 | 4.0 | 15 | 7.9 | 75 | 71.6 | 1 | 1.9 | 0 | 0.8 | 7 | 6.3 | 4 | 5.5 | 4 | 12.8 |
| S. minutus | 10 | 4.0 | 0 | 1.6 | 4 | 2.3 | 27 | 20.2 | 2 | 0.7 | 0 | 0.3 | 0 | 1.2 | 4 | 1.7 | 7 | 5.5 |
| N. fodiens | 0 | 0.8 | 0 | 0.1 | 0 | 0.5 | 2 | 2.0 | 0 | 0.0 | 0 | 0.1 | 0 | 0.2 | 0 | 0.1 | 0 | 0.7 |
| M.musculus | 0 | 0.2 | 0 | 0.1 | 1 | 0.1 | 6 | 1.3 | 0 | 0.0 | 0 | 0.0 | 1 | 0.4 | 7 | 2.3 | 64 | 15.9 |
| C. glareolus | 114 | 173.4 | 1 | 7.8 | 28 | 33.2 | 40 | 60.8 | 2 | 6.3 | 3 | 2.9 | 74 | 89.3 | 18 | 33.1 | 23 | 54.1 |
| A. agrarius | 16 | 4.9 | 2 | 2.3 | 5 | 2.7 | 147 | 149.9 | 4 | 2.7 | 2 | 0.6 | 19 | 12.5 | 56 | 31.7 | 19 | 19.9 |
| A. flavicollis | 100 | 67.5 | 14 | 5.1 | 0 | 4.7 | 49 | 50.0 | 7 | 5.2 | 0 | 1.3 | 118 | 109.4 | 42 | 44.9 | 57 | 37.6 |
| A. uralensis | 1 | 0.9 | 0 | 0.0 | 0 | 0.3 | 0 | 1.8 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| M. minutus | 5 | 0.6 | 4 | 0.3 | 1 | 0.5 | 65 | 16.2 | 5 | 0.4 | 1 | 0.0 | 5 | 1.5 | 4 | 1.5 | 5 | 1.0 |
| A. oeconomus | 2 | 1.6 | 0 | 0.6 | 0 | 1.0 | 49 | 68.0 | 1 | 3.4 | 0 | 0.2 | 0 | 1.5 | 0 | 6.3 | 1 | 1.6 |
| M. arvalis | 1 | 2.4 | 0 | 0.6 | 2 | 1.2 | 42 | 56.4 | 0 | 0.8 | 0 | 0.3 | 0 | 0.4 | 45 | 48.6 | 11 | 39.0 |
| M. agrestis | 6 | 3.9 | 0 | 0.5 | 0 | 1.7 | 11 | 14.9 | 0 | 0.6 | 1 | 0.6 | 1 | 2.3 | 1 | 5.3 | 0 | 3.0 |
| Total | 273 | 273 | 23 | 23 | 56 | 56 | 513 | 513 | 22 | 22 | 7 | 7 | 225 | 225 | 181 | 181 | 191 | 191 |
| χ^2 | 107.7 *** | | 71.6 | *** | 27.7 *** | | 185.4 *** | | 63 *** | | 6.5 NS | | 19.8 * | | 53.2 *** | | 219.9 *** | |

Table A2. Observed and expected frequencies of individuals with BCI > 4 in different small mammal species depending on habitat. Green cells: observed frequencies \geq 3 times more than expected ones; brown cells: observed frequencies \geq 3 times less than expected ones; ***—p < 0.0001, *—p < 0.05, NS—not significant.

Table A3. Observed and expected frequencies of individuals with BCI > 5 in different small mammal species depending on habitat. Green cells: observed frequencies \geq 3 times more than expected ones; brown cells: observed frequencies \geq 3 times less than expected ones; ***—p < 0.001, **—p < 0.001, NS—not significant.

| Species with | For | est | Shr | ub | Wetland | | Meadow | | Riparian | | Mixed | | Disturbed | | Agricultural | | Commensal | |
|----------------|------|------|-----|-----|---------|-----|-----------|------|----------|-----|-------|---------|-----------|--------|--------------|----------|-----------|-----|
| BCI > 5 | Obs | Exp | Obs | Exp | Obs | Exp | Obs | Exp | Obs | Exp | Obs | Exp | Obs | Exp | Obs | Exp | Obs | Exp |
| S. araneus | 1 | 1.0 | 1 | 0.2 | 0 | 0.3 | 8 | 9.2 | 1 | 0.4 | 0 | 0.0 | 1 | 0.6 | 0 | 0.2 | 0 | 1.1 |
| S. minutus | 4 | 0.3 | 0 | 0.1 | 1 | 0.1 | 5 | 2.6 | 0 | 0.2 | 0 | 0.0 | 0 | 0.1 | 1 | 0.0 | 0 | 0.5 |
| N. fodiens | 0 | 0.1 | 0 | 0.0 | 0 | 0.0 | 0 | 0.3 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 0 | 0.1 |
| M.musculus | 0 | 0.0 | 0 | 0.0 | 1 | 0.0 | 1 | 0.2 | 0 | 0.0 | 0 | 0.0 | 1 | 0.0 | 0 | 0.1 | 9 | 1.4 |
| C. glareolus | 4 | 14.0 | 0 | 0.3 | 0 | 1.2 | 1 | 7.8 | 1 | 1.4 | 0 | 0.0 | 8 | 8.7 | 0 | 0.9 | 1 | 4.8 |
| A. agrarius | 2 | 0.4 | 0 | 0.1 | 0 | 0.1 | 12 | 19.3 | 0 | 0.6 | 0 | 0.0 | 1 | 1.2 | 3 | 0.9 | 1 | 1.8 |
| A. flavicollis | 8 | 5.4 | 0 | 0.2 | 0 | 0.2 | 6 | 6.4 | 2 | 1.2 | 0 | 0.0 | 9 | 10.7 | 0 | 1.2 | 4 | 3.3 |
| A. uralensis | 0 | 0.1 | 0 | 0.0 | 0 | 0.0 | 0 | 0.2 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 | 0 | 0.0 |
| M. minutus | 2 | 0.0 | 0 | 0.0 | 0 | 0.0 | 18 | 2.1 | 1 | 0.1 | 0 | 0.0 | 2 | 0.1 | 1 | 0.0 | 0 | 0.1 |
| A. oeconomus | 0 | 0.1 | 0 | 0.0 | 0 | 0.0 | 12 | 8.7 | 0 | 0.8 | 0 | 0.0 | 0 | 0.1 | 0 | 0.2 | 0 | 0.1 |
| M. arvalis | 0 | 0.2 | 0 | 0.0 | 0 | 0.0 | 2 | 7.3 | 0 | 0.2 | 0 | 0.0 | 0 | 0.0 | 0 | 1.3 | 2 | 3.5 |
| M. agrestis | 1 | 0.3 | 0 | 0.0 | 0 | 0.1 | 1 | 1.9 | 0 | 0.1 | 0 | 0.0 | 0 | 0.2 | 0 | 0.1 | 0 | 0.3 |
| Total | 22 | 22 | 1 | 1 | 2 | 2 | 66 | 66 | 5 | 5 | 0 | 0 | 22 | 22 | 5 | 5 | 17 | 17 |
| χ^2 | 62.6 | *** | 3.9 | NS | 10.0 | NS | 140.7 *** | | 11.5 NS | | | 37.1 ** | | 8.9 NS | | 47.6 *** | | |

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