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Transition of Small Mammals from Live Elements of the Biocenoses to a Subfossil State

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Abstract—A wide range of problems arising during paleoreconstructions of small mammal communities and individual animal characteristics is reviewed. The patterns of transformation and information loss at the stages of the transition of small mammals from live elements of biocenoses to a subfossil condition through the stage of prey of birds-myophages are discussed. A literature analysis shows the capacities and limitations of modern methods for reconstructing the sizes, ages, and diets of small mammals based on their molars. The digestive secretions of owls that affect the morphological and size parameters of the remains of the small mammals they consume are discussed. Particular attention is paid to the processes in which animal bone remains become part of the deposits and are transformed to subfossils. Transformations of the characteristics of small mammalian communities and the intraspecific structure of species as selective prey to raptors are shown. The importance of considering the differentiated loss of bone remains of different sizes that occurs during their digestion and dispersion in deposits is demonstrated.

Keywords: small mammals, owls, food selectivity, taphonomy, animal size, age, diet, paleoreconstructions

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INTRODUCTION

One of the urgent tasks of modern biology is to predict the dynamics of ecosystems in connection with global climatic changes. A large complex of approaches and methods is used to solve it, including the method of historical analogies of past events. It is especially important to understand the processes that took place in the Holocene (10–0 Kyr), because they affect modern communities. This period is studied by historical ecology. A great contribution to the development of historical ecology was made in the second half of the 20th century by L.G. Dinesman. We dedicate our work to the 100th anniversary of the birth of this remarkable scientist and person.

Currently, the direction of historical ecology aimed at improving the procedures of ecological reconstructions by assessing the degree and forms of transformation and reduction of information during the transition of small mammals from live elements of the biocenoses to the subfossil state is under development. Research in this area is at the intersection of ornithology, theriology, developmental biology, and taphonomy.

Almost any aspect studied by historical ecology goes through the preliminary stages of research on modern material, when its informative value for paleoreconstructions, as well as the degree of information distortion and data errors, is assessed. The direction of research to which this work is devoted covers the previous and initial stages of the taphonomic process in ornithogenic sediments and includes several sections. The first section covers the study of living objects as part of the biocenoses. The second section is devoted to study of their ornithogenic transformation (the selectivity with which animals become prey to raptors and the destruction of their bone remains and teeth during digestion). The first two sections include research in nature and simulation of some processes under experimental conditions. The third section is devoted to study of the initial stages of the taphonomic process. It is based on the study of modern ornithogenic deposits formed and averaged over several decades in comparison with the data of long-term monitoring of the small mammal population. This article is dedicated to reviewing the problems that are faced in paleoreconstructions of small mammal communities and individual characteristics of animals associated with the transition of living organisms into the subfossil state.

RECONSTRUCTION OF THE SIZE, AGE, AND MORPHOLOGICAL CHARACTERISTICS OF SMALL MAMMALS ON THE BASIS OF ODONTOLOGICAL CHARACTERS

To clarify and detail paleontological reconstructions, it is necessary to identify the sources of errors associated with the growth and life activity of animals. Determination of the magnitude of these errors and the development of methods for their elimination are the purpose of this section.

Reconstruction of animal sizes. Size is one of the characteristics that allow making judgments on a number of ecological, physiological, evolutionary, and other characteristics of animals (Schmidt-Nielsen, 1987; Martin, 1996; Hopkins, 2018). The size of a mammal is most often characterized by its weight and, less often, by its body length. Reconstruction of the size of small mammals is performed in both neontological and paleontological studies. Determination of the size of extant animals by bone remains is sometimes necessary (for example, when studying the selectivity of feeding of raptors). Researchers obtain especially accurate results of reconstructions when they assess the size using the bones of animals caught in the hunting areas of the birds studied (Balčiauskas and Balčiauskienė, 2014, 2014a).

The sizes of extinct animals are reconstructed using an actualistic approach (determination of the allometric relationship between the skeletal dimensions and the dimensions obtained for modern species) (Freudenthal and Martín-Suárez, 2013). The secular variability of the body size of mammals can be studied on subfossil remains from excavations and in museum collections (Yom-Tov and Yom-Tov, 2004). Fluctuations in the body size of mammals during the cold and warm epochs of the Pleistocene and Holocene are the subject of research in paleozoological works (Lozano-Fernández et al., 2013; Bertrand et al., 2016).

For the majority of small-mammal species, molars are the most commonly used paleontological material. This is due to both the possibility of species diagnostics and the best preservation of these parts of the skeleton. Paleontologists often work with isolated teeth, being unable to measure the cranial and postcranial elements of the skeleton and select the most informative bones for reconstructing the animal body size (Fortelius, 1990; Borowski et al., 2008). Thus, the size of animals is judged by the size of their isolated teeth (usually the first lower molar (m1)). To estimate the size, the length and width of the occlusal surface and the length of the crown from the lateral surface are measured. The principles of reconstructions of the body size of fossil mammals and the problems arising from such studies are described in several summarizing papers (Damuth et al., 1990; Fortelius, 1990; Freudenthal and Martín-Suárez, 2013; Hopkins, 2018). We will mention the problems highlighted in the listed works in a thesis form, focusing mainly on those aspects that are associated with the growth and functioning of teeth during an animal's life.

In describing the size for a species in general, the changes in weight over the seasons, as well as the sex- and age-related differences that affect the individual size of the animal, are not essential (Hopkins, 2018). The ratio between the body size and the size of skeletal parts is different in different taxonomic groups of animals (Gould, 1975; Hopkins, 2018). Such differences have been shown for the families of rodents (Hopkins, 2008, 2018; Freudenthal and Martín-Suárez, 2013). Therefore, it is easier to reconstruct the size of an animal when there is a modern member of the same species to create a training group. When the task is to reconstruct the size of an extinct species, it is complicated by the fact that the allometric ratios of its teeth and body size may be different from that in extant related species (Millien and Bovy, 2010; Hopkins, 2018).

One of the main difficulties in reconstructing individual sizes is the relatively weak relationship between the sizes of the body and of a tooth at the intraspecific level. For example, in the groups of root voles homogeneous in the molar size, the scatter of the body length values reached 60 mm. Pearson's correlation coefficient between the molar and body length varied widely in samples from different regions of the Urals and Yamal (Kropacheva et al., 2015). The task is complicated by the fact that the ratio between the body and molar sizes changes with age. This phenomenon most is clearly manifested in the molars of animals with have a high crown that do not form roots (hypselodont type of tooth structure). In these animals, the tooth continues to grow in height throughout life and in length for a significant part of life.

In a number of studies on *Microtus* voles, which were performed by different methods, the growth parameters of teeth and the body were investigated. Such data were obtained for the root vole (Kropacheva, 2013, 2015), the narrow-headed vole (Kropacheva, 2016), and the common vole (Balčiauskienė, 2007). According to the well-known allometric pattern, the growth of an organism in relative values outstrips the growth of individual organs (Klevezal, 2007). The body growth in the first months of life in percent significantly outstrips the tooth growth in length but lasts for a shorter period of time. The ratio of the molar length to the body length decreases during the period of intensive body growth, slightly increases during the period when the body growth is completed but the tooth continues to grow in length, and stabilizes when the growth of both the body and the tooth is completed (Kropacheva, 2013; Kropacheva et al., 2015, 2016). Accordingly, immature animals have larger teeth in relation to the body size than adult ones.

In the root-toothed forms of voles, the growth of the crown both in length and in height ceases during the formation of roots. For these species, changes in the size of teeth with age associated with the wear of teeth rather than their growth were described. Using several examples, it was shown that the length of the occlusal surface increases with age (Balčiauskienė, 2007a; Kropacheva et al., 2017). This may be due to both the shape of the crown and the change in the grinding angle of the tooth with age.

The growth parameters of voles vary greatly. According to the results of study of animals from laboratory colonies, several types of body growth and cranial structures were identified (Balčiauskienė, 2007a; Kropacheva, 2013, 2016). In animals with different types of body growth, the molar length indices differ. Using the root vole as an example, it was shown that, for a relative similarity of the tooth growth parameters, the differences in the indices were determined primarily by the body growth parameters. The voles with slow and short-term growth had the most peculiar characteristics—the highest allometry index and the lowest correlation coefficient between the molar and body lengths. In the voles from one to three months old, the largest relative sizes of molars are observed in the animals with fast and long-term body growth, whereas in the animals older than four months, the largest relative sizes of molars were observed in the voles with slow and short-term body growth (Kropacheva, 2015). These data make it possible to assess the direction of bias in the estimates of the body size by the molar size under the influence of two factors—the individual age and the type of growth of the animal. Since immature animals have relatively large molars, their abundance in a sample leads to an overestimation of the body size. The same bias in the assessment is caused by the use of teeth of animals with a slow and short-term type of body growth, which, similarly to the immature animals, have larger relative tooth sizes.

In nature, the growth parameters of rodents differ in animals from different generations. Growth processes slow down in autumn and winter. It was shown (Shvarts, 1969; Olenev, 2002; Olenev and Grigorkina, 2014) that, among many factors that determine the size of individuals in populations of cyclomorphic rodents, the most important factor is the affiliation to one or another seasonal generation or functional group. The majority of voles live in nature for only several months, but the calendar and physiological ages in different generations may differ significantly (Olenev, 2002; Ivanter, 2015). For animals with cyclical changes in abundance, differences in growth parameters at different phases of abundance were shown (Zejda, 1971; Burtheet al., 2010; Petrová et al., 2018).

Another obstacle in studying the size of the teeth is determined by the variation in the grinding angle of the occlusal surface and the associated changes in the occlusal surface length. Using the root vole as an example, it was shown that the grinding angle of the occlusal surface varies from 57° to 88°. Differences between the samples from different regions of the Urals were revealed on the basis of the grinding angle values (Kropacheva et al., 2015). This problem can be solved easily by measuring the tooth from the lateral surface rather than from the occlusal one. Unfortunately, in this case, the possibility of comparison with measurement data obtained by other authors is lost, because the method of measurement from the occlusal surface of the tooth is more common than measurements from the lateral surface. In addition, in some cases, it is impossible to measure a tooth from the lateral surface (for example, when taking intravital dental impressions). Therefore, when measuring a tooth from the occlusal surface, it makes sense to take into account the error associated with variations in the grinding angle and preliminarily estimate it for the species of interest.

The size of the occlusal surface of molars decreases with the appearance of lateral wear facets. This functionally conditioned pathological formation is widespread in nature (Smirnov and Kropacheva, 2015). In the study of animals under laboratory conditions, it was shown that the length of the occlusal surface decreased to 7% in root voles and to 5% in narrow-cranial voles (Smirnov and Kropacheva, 2015).

Thus, the statement of the fact that there is a positive correlation between the body and molar sizes does not provide sufficient grounds for an individual quantitative assessment of the body size by the m1 size. In reconstructing the size of animals by the size of a tooth, it is necessary to know the ratio of these values obtained on extant animals. For more accurate reconstructions of individual sizes, it is necessary to take in to account the age of the animal (dividing individuals into age groups), as well as the difference in size due to different grinding angles of the occlusal surface and the development of lateral wear facets. In addition, it is necessary to take into account the changes in the tooth sizes associated with the digestion by raptors.

Determination of the age of animals based on the morphological parameters of the teeth. The problem of determination of the age of small mammals by assessing the morphology of skeletal structures subject to ontogenetic changes is widely studied (Olenev, 1989; Evdokimov, 1997; Klevezal, 2007). The principles and methods for determination of the age of mammals are summarized in the monograph by Klevezal (2007). In the bunodont rodents, age groups are most often distinguished by the degree of enamel wear and dentin exposure (Klevezal, 2007). The age criterion for the hypsodont forms is the development of the roots of molars and the ratio between the crown height and root length. The difficulty of determining the age by the tooth root length is due to the fact that, in voles of different generations, tooth roots grow at different rates (Olenev, 1989; Evdokimov, 1997). The determination of the age of extant animals by assessing the development of tooth roots is performed taking into account the generative state and the season of birth (Olenev, 1989, 2009; Evdokimov, 1997). For fossil animals, studies are based only on the characteristics of the teeth, which causes a greater error in age determination as compared to the extant animals. To determine the age, growth parameters, season of death, and a number of other life-cycle characteristics, methods for assessing the recording structures (growth layers in the bone tissue and teeth of mammals) were developed. An overview of these methods is given in a dedicated paper (Klevezal and Smirina, 2016). It was shown that the season of death of some species of rodents and their relative age can be estimated from the thin sections of the lower jaw by assessing the state of the bone tissue of the mandible and the molar cementum (Klevezal, 2001). This technique was used to analyze the remains of mice of the genus *Apodemus* from the pellets of the *Microtus* owl *Strix aluco* (Klevezal and Pucek, 2007).

In the techniques where the criterion for the age of rodents is the wearing of teeth or the ratio between the crown height and root length, an error may arise due to different wearing rates during life and eating food of different degrees of abrasiveness (Egorov, 1958; Kropacheva et al., 2016). In addition, it is necessary to take into account the changes in the size of dental tissues of different densities associated with digestion by the raptor accumulating the material.

Assessment of morphological features of the occlusal surface of molars. The morphological characteristics of the teeth give an idea of the food specialization of the animal, its taxonomic affiliation, and age. They are also used to study the patterns of the evolutionary process, the effect of isolation, and the impact of long-term declines in abundance (Chaline et al., 1999; Borodin, 2009; Agadzhanyan, 2012; Markova and Smirnov, 2018).

Numerous features characterizing the shape of the occlusal surface of vole teeth, as a rule, are assessed by isolating morphotypes. The analysis of this approach and the unification of the morphotypes of vole teeth with allowance for evolutionary and ontogenetic factors were performed in a series of studies (Markova, 2013; Markova et al., 2018). In these papers, to distinguish morphotypes in the family Arvicolinae, it was proposed to use indices such as the number of outgoing and incoming angles on the lingual and buccal sides of the cheek teeth, as well as the presence or absence of the corresponding fields on the occlusal surface (Markova, 2013). A more specialized scheme was developed for the tribe Lemmini (Markova et al., 2018).

In certain approaches, the age component may contribute to the assessment of morphological variability. In root-toothed and non-root-toothed animals, the age-related variability has different nature. The age-related changes are most pronounced in the root-toothed (especially bunodont) forms, in which this is the simplest process. It is associated only with wearing of the crowns with age, because the crown does not grow in height during the animal's life due to the early laying down of roots in ontogeny. In this case, all age-related changes are associated with the shape, size, and relative position of the tubercles. More complex processes of crown growth and wear are observed in the root-toothed hypsodont voles. It is also associated primarily with wearing the crown with age. However, the tooth neck in such species is formed at the early stages of post-juvenile ontogeny (*Evropeiskaya ryzhaya polevka* ..., 1981). Wear is accompanied by changes in the occlusal surface pattern (Viriot et al., 2005; Guérécheauet al., 2010; Ledevin et al., 2010). When the occlusal surface approaches the tooth neck, all the prisms fuse, and the pattern is lost completely (Klevezal, 2007).

Another factor that causes the age-related changes is the continued growth of the crown in height. This process is observed in the hypselodont forms. The growth rate of molars in different species of non-root-toothed vole forms varies from 0.078 to 0.17 mm per day, whereas, for example, in the bank vole (root-toothed vole), the growth rate of molars is 0.007 mm per day (Golenishchev and Kenigswald, 1978; Kropacheva et al., 2012). Intensive increase in the length of molars in length in *Microtus* voles continues up to 4–5.5 months (Kropacheva, 2013, 2016). Changes in size are accompanied by morphological changes; they were described for several species of voles, as well as for lagomorphs.

Age-related changes manifested in the simplification of the contour of the occlusal surface of molars were found in Lagomorphs (Angelone et al., 2014). A study performed on brown lemmings showed that the age-related changes are directed towards the development of elements that appear at the initial stages of ontogeny (Cheprakov, 2010). The age-related variability of molars was described for several species of *Microtus* voles—the Middendorf vole (Kourova, 1985), the root vole (Kropacheva et al., 2012), and the narrow-headed vole (Markova et al., 2013; Kropacheva, 2015). Studies devoted to the age variability of m1 of the root vole showed that the period from 1 to 12 months is characterized by a tendency towards smoothing of the additional external reentrant angle on the anterior unpaired loop of m1 and an increase in the fourth external exiting angle (Kropacheva et al., 2012). In the narrow-headed vole, a decrease in the depth of the reentrant angles on the anterior unpaired loop was detected. In rare cases, during the animal's life, changes in the occlusal surface shape were so significant that, at different ages, it could be attributed to different morphotypes assessed according to the Markova scheme (2013). The majority of age-related changes occurred either in the area of one morphotype or affected the area of the main and transitional morphotypes (Markova et al., 2013; Kropacheva, 2015).

Thus, the magnitude of the error associated with the age-related changes depends partly on the technique for morphotype identification. If the division is too fractional and includes numerous transitional forms, the age-related variability may play a significant role. If morphotypes are distinguished using meristic characters (Markova, 2013), the age-related changes in the occlusal surface shape often occur within the same morphotype (Kropacheva, 2015). Therefore, these changes are not a serious problem in the study of tooth morphology if the morphotypes are distinguished using the correct technique. Moreover, the age-related changes in the occlusal surface characteristics can be used as criteria for the individual age of animals. Using this approach, it seems promising to solve the problem of dividing the teeth of the non-root-toothed voles into age groups by distinguishing the characters that can be used to separate immature and adult animals (Kropacheva, 2016).

Reconstruction of characteristics of the animal diet. The features of the diet of small mammals reflect not only the type of tooth structure but also the shape of the occlusal surface relief of their molars (Rodrigues et al., 2013; Ulbricht et al., 2015; Kropacheva et al., 2016; Burgman et al., 2016; Calandra et al., 2016; Zykov et al., 2018). The results of microwear and mesowear analysis do not allow assessing the species composition and ratio of food items. However, using these results, it is possible to identify the main components of the diet differing in abrasiveness and density: plants with a high and low phytolith content, seeds, berries, and insects. Mesorelief is a form of dental structures that occurred during functioning due to wear to the working surface. The mesorelief reflects weeks and months of keeping to a certain diet and is suitable for assessing the geographical and temporal trends in animal nutrition. The mesowear analysis was developed for selenodont and trilophodont ungulate mammals (Fortelius and Solounias, 2000) and became widespread in the study of large mammals. Differences in the structure of the teeth of small mammals, the biomechanics of chewing movements, and trophic specialization of different taxonomic groups imply different approaches to mesowear analysis. The information content of the mesorelief as an indicator of a number of dietary characteristics was shown in bunodont, hypsodont, and hypselodont rodents and lagomorphs (Lee and Houston, 1993; Sibiryakov, 2013; Müller et al., 2014; Smirnov and Kropacheva, 2015; Ulbricht et al., 2015; Kropacheva et al., 2016).

The signs that characterize the density and abrasiveness of the diet components of the hypselodont *Microtus* voles are the height of the teeth above the alveoli, the grinding angle of the occlusal surface relative to the anterior surface of the molar, lateral wear facets, the shape of the occlusal surface relief, and large chips (Lee and Houston, 1993; Smirnov and Kropacheva, 2015; Kropacheva et al., 2016). For bunodont and hypsodont species, different variants of the occlusal surface relief shape were described (Lee and Houston, 1993; Ulbricht et al., 2015).

Microrelief is microdamage to the enamel and, less often, dentin that occurs during chewing. It characterizes the diet during hours and days of an animal's life (Belmaker, 2018). Microwear analysis is widely used in reconstructing the diets of various taxonomic and trophic groups of animals, including small mammals. The use of microwear analysis for small mammals was reviewed by Belmaker (2018). In addition to obtaining information about the diet, microscratches are used to determine the direction of the chewing movements of animal's jaws (Charles et al., 2007). The microrelief characteristics that are used for paleoreconstructions of the vole diet are the number and direction of microscratches, the number of fosses and chips, and the area of damage to the anterior enamel wall of the teeth (Ungar et al., 2008; Zykov et al., 2018). Microrelief is studied by electron microscopy and 3D microsurface analysis (Calandra and Merceron, 2016).

In this direction, experimental studies on the effect of different food items on the microrelief and mesorelief of teeth are of great importance. However, such studies are fairly scanty. In an experiment on rabbits and guinea pigs, the microrelief features that formed when the animals were kept on diets containing different amounts of plant phytoliths in dry and wet food were described (Schulz et al., 2013; Winkler et al., 2019). It was found that the growth and wear of the teeth of domestic rabbits and guinea pigs vary depending on the consumption of internal and external abrasives and that these two processes are closely interrelated (Müller et al., 2014, 2015).

Experimental studies on *Microtus* voles showed the types of microwear and mesowear formed when using feed of different densities and abrasiveness. It was found that eating low-abrasive food led to the appearance of signs of tooth-to-tooth wear (grinding): a low crown, a more obtuse grinding angle of m1, a shallow relief of the occlusal surface, a larger area of damage to the enamel wall, and lateral wear facets. In eating abrasive food, the decisive factor was the interaction of teeth with food. The voles that were kept on abrasive-food had a higher crown, a sharper grinding angle of m1, a deeper relief of the occlusal surface, the absence of lateral wear facets, and more intact tooth enamel. When food contained dense components, which required pressing movements during chewing, a fossa affecting mainly reparative dentin was formed (Smirnov and Kropacheva, 2015; Kropacheva et al., 2016; Zykov et al., 2018).

Variations in mesowear patterns were shown in a few studies performed on small mammals from modern natural populations, (Sibiryakov, 2013; Ulbricht et al., 2015), and variations in microwear patterns of teeth were shown in a large number of studies (Patnaik, 2002; Nelson et al., 2005; Gomes-Rodrigues et al., 2009; Rodrigues et al., 2009; Burgman et al., 2016; Calandra et al., 2016; Winkler et al., 2016). These and experimental data are used for reconstructions of the diet of fossil animals. There are a few works devoted to mesowear analysis of the teeth of small mammals on fossil materials (Fraser and Theodor, 2010) and a number of works on microwear analysis. In the cases when species of extant animals are studied, the microwear patterns of their teeth from localities are compared with the teeth of modern representatives of the same species (Lewis et al., 2000). When reconstructing the diet of an extinct species, the microwear pattern of its teeth is compared with the microrelief types that were identified for the modern related species (Charles et al., 2007; Townsend and Croft, 2008; Hautier et al., 2009; Rodrigues et al., 2009; Firmat et al., 2011; Kaya and Kaymakci, 2013).

Unlike the methods developed for microwear analysis, methods for mesowear analysis of the teeth of small mammals are at the initial stages of development. Further experimental work on different groups of animals is required to accumulate basic knowledge on the growth and wearing processes, which are necessary for the transition to paleoreconstructions of diets on the basis of this knowledge.

In modern research, tooth wear analysis is combined with other methods. The combination of methods of microwear analysis and analysis of the carbon isotopic composition made it possible to determine the relative proportions of plants with different types of photosynthesis in the diets of two extinct herbivorous rodent species (Hopley et al., 2006). The combination of methods for the analysis of the morphological structures of teeth and microwear patterns were used to study food adaptations of rodents in the course of evolution (Charles et al. 2007; Rodrigues et al., 2013).

ORNITHOGENIC TRANSFORMATION OF COMMUNITIES AND INDIVIDUAL CHARACTERISTICS OF SMALL MAMMALS

Among birds of prey, the most frequent agents for the accumulation of bone remains of small mammals are owls (Andrews, 1990). Ornithogenic sediments are formed on the basis of pellets produced by birds of prey in places of long-term nesting or in places of their perches. The most favorable places of pellet accumulation are confined to caves and grottoes in rock massifs. The composition and ratio of the remains of small mammals in ornithogenic sediments are not identical to them in natural communities. Reconstruction of the fauna and structure of the animal population on the basis of such materials requires taking into account the selectivity of their prey, which depends on various factors. For this purpose, neontological studies of the transformation of the composition and structure of the population of small mammals into a subfossil state through the feeding activity of owls in the field conditions are performed. The preservation of bone material depends on the degree of influence of the digestive enzymes of birds and factors of fossilization. This aspect is studied using a set of experimental neontological approaches.

Transformation of small-mammal communities. One of the main tasks of historical ecology is the reconstruction of animal and plant communities of the past. Leading experts in taphonomy of ornithogenic sediments in their works emphasize the importance of an actualistic approach to taphonomic studies (Andrews, 1990; Terry, 2008, 2010; Lyman, 2012; Andrews and Fernández-Jalvo, 2018). Studies of the feeding behavior of owls are performed in combination with the estimations of small-mammal populations and biotopic characteristics of the locality (Smirnov and Sadykova, 2003; Terry, 2008, 2010; Andrews and Fernández-Jalvo, 2018). The species composition of owl prey may include almost all representatives of mammalian fauna; however, for each predator species, there is a dimensional and biotopic range of prey (Mikkola, 1983; Andrews, 1990; Shepel, 1992; Pukinskii, 1993; Balčiauskienė et al., 2005; Shokhrin, 2008; Terry, 2010; Heisler et al., 2016). The main problem in reconstructions is the food selectivity of owls, which manifests itself in the differences in the proportion of species in a community and in the diets of birds. The food selectivity and the dynamics of the diet of birds of prey are widely investigated in ornithological studies. The diet of predators depends on a complex of factors, such as the abundance, biotopic confinement, social structure, behavioral characteristics, size, and taxonomic affiliation of prey (Korpimäki and Sulkava, 1987; Trejo and Guthmann, 2003; Comay and Dayan, 2018b). The ratios of the proportions of small-mammal species in the communities and in the diet of owls are similar in open landscapes (Terry, 2009, 2010). In landscapes with alternating open and closed habitats in the diet of owls, both the species preferences and the degree of availability of prey are reflected to a greater or lesser extent depending on food specialization (Korpimäki and Sulkava, 1987; Sadykova and Smirnov, 2005; Comay and Dayan, 2018b). Owls include both specialized and versatile predators. Bone remains of small mammals are accumulated by a number of species (eagle owls, barn owl, snowy owl, several species of the genus *Strix*, long-eared owl, etc.), each of which shows unique features of food selectivity during hunting (Andrews, 1990). For some species of owls in which the foraging behavior is closest to opportunistic, positive correlations between the ratios of the proportions of the majority of species in the diet and in the natural community were shown. Nevertheless, even in these cases, their proportions are not identical to each other, and food selectivity is observed (Tores et al., 2005; Balčiauskienė and Naruševičius, 2006). Usually, ornithologists conditionally distinguish groups of prey in the structure of the diet of raptors. The diet is dominated by the main prey items (one or more species belonging to the most preferred size and biotopic group) (Korpimäki and Sulkava, 1987; Korpimäki, 1992). In cases of insufficient abundance of the main prey items in the diet, the proportion of alternative prey items increases.

They have a number of features that make them less preferred prey objects: they are smaller in size, live in biotopes less accessible for hunting, and hunting them is more energy-intensive for owls (Korpimaki, 1992; Zárybnická et al., 2009). These two groups of prey items make up the largest fraction of the diet, both in terms of the number of individuals caught and by their weight. In terms of the number of species, the third group predominates, which is proposed to be called concomitant prey (Smirnov and Kropacheva, 2019). They inhabit biotopes that are rarely inspected by birds (not only hunting but also transit areas) and/or are beyond the preferred range in weight. This group is rarely considered in detail by ornithologists but is of great interest for paleoecological studies. Both the major and alternative prey items are usually abundant species; however, the composition of accompanying prey also often includes the dominant species of the small-mammal community. These species function as indicators of the presence of a number of habitats in the surrounding landscape that are secondary for the foraging activity of predators, but their detection is important for paleoreconstructions (Smirnov and Kropacheva, 2019; Smirnov et al., 2019). Consideration of the prey of predatory owls as a source of accumulation of paleotheriological materials leads to the conclusion that the most important aspect of selectivity is the selection of hunting biotopes (Comay and Dayan, 2018; Smirnov and Kropacheva, 2019; Smirnov et al., 2019). In addition, bone remains in ornithogenic sediments are usually accumulated during the breeding period. During this period, more than the rest of the time, the diet is influenced by the biotopic characteristics of the foraging ground, because its area is reduced (Bull et al., 1988; Van Riper and van Wagtendonk, 2006; Penteriani et al., 2015).

The approach to the reconstruction of communities of extinct small mammals when data on the modern communities of small mammals and their environment are compared with the composition of pellets produced by modern owls in order to analyze their correspondence seems to be the most logically completed. The data obtained are used in paleoreconstructions based on the pellets produced by the extinct birds that inhabited the same territory in the past (Comay and Dayan, 2018). On the basis of the comparison of paleontological and neontological data, the current state of the community is assessed, the factors that have the greatest influence on it are identified, and changes in the communities in the future are predicted (Terry, 2008; Rowe and Terry, 2014).

Transformation of the intraspecific structure of the population of small mammals. Reconstructions of the intraspecific structure of the population of small mammals (size, age, and gender) also face the selectivity of owls (Donazar and Ceballos, 1989; Karell et al., 2010; Sunde et al., 2012; Balčiauskas and Balčiauskienė, 2014). The sizes of prey vary in different seasons and/or in the breeding and nonbreeding periods (Trejo and Guthman, 2003; Trejo et al., 2005; Korpimäki, 1986; Romanowski and Żmihorski, 2009) as well as during the breeding period (Wellicome et al., 2013). Thus, when reconstructing the size of animals on the basis of ornithogenic sediments, it is necessary to take into account the consequences of this selectivity by studying it in species that accumulate the material.

To study intraspecific selectivity, approaches from the standpoint of both ornithology and theriology are applied. An important component in this area of research is the determination of the size, sex, and age of animals from isolated parts of the skeletons (Trejo et al., 2005; Balčiauskas and Balčiauskienė, 2014; Lyman et al., 2016). Attempts were made to use the methods developed on modern animals and adapted to ornithogenic paleontological materials, to estimate the size and the age composition of prey from sediments, and to establish the reasons for selectivity (Kropacheva, 2016; Kropacheva et al., 2017).

Destruction of bone material and teeth as a result of digestion. Preservation of bone material, which depends on the degree of influence of the digestive enzymes of the predator, is studied in paleontology when determining the agent of the accumulation of bone remains (Andrews, 1990; Fernández-Jalvo et al., 2016; Comay and Dayan, 2018a; Terry et al., 2018). The bone remains of the prey of owls (in particular, the eagle owl) differ from the food remains of four-legged predators by their good preservation (Andrews 1990; Terry, 2007). A series of works describes in detail the features of the preservation of the skeletal elements and teeth in pellets of different owl species (Andrews 1990; Terry et al., 2018; Terry, 2007; Lyman, 2018). A classification of predators by the degree of modification of the bone remains of prey (Andrews, 1990) and classification of the degree of tooth damage (Andrews, 1990; Fernández-Jalvo et al., 2016) were proposed. A taphonomic index for determination of the accumulation agent by bone damage was developed (Comay and Dayan, 2018a).

However, while providing valuable information in determining the agent for material accumulation, erosion destroys a number of sources of information used in paleoreconstructions. This aspect of the problem is solved using a set of experimental neontological approaches. The selectivity of preservation of both skeletal elements and bones of animals of different ages was described (Sharikov et al., 2018). It was shown that the degree of destruction of the remains after digestion by owls differs in different seasons (Andrews and Fernández-Jalvo, 2018). There is evidence that digestion becomes more intense when the food supply is insufficient. It can be assumed that the loss of bone material during digestion increases in the periods of lack of food.

Rodent teeth consist of tissues of different hardness. The hardest is enamel, followed by dentin of varying density and cement. At the initial stages of digestion, when the teeth are in the alveoli, the substances of the digestive system affect the tooth crown. Dissolution begins from protruding surfaces (the outgoing corners of enamel prisms or tubercles); in the presence of cement and dentin on the occlusal surface, they are also exposed to acids (Fernández-Jalvo et al., 2016). At the subsequent stages of digestion, the tooth falls out of the alveoli of the broken jaws; then, the roots are also digested. Thus, if the tooth remains in the alveolus, the ratio of the root length to the crown height can be altered due to the decrease in the crown size. In the case when the tooth was isolated during digestion, and the digestion of the root part began, the ratio changes due to the dissolution of both the crown and the root. The possibility of such changes should be borne in mind when using methods for determination of the age by the dental structures on paleontological material.

In an experimental study, it was shown that, during digestion, the size of the tooth crown decreases already at the initial stages of destruction, which may introduce an error in the reconstruction of the size of animals. Destruction of the surface layers of the enamel and dentin of the occlusal surface leads to a loss of data on microwear of teeth, and mesowear remains unchanged only on well-preserved teeth (Kropacheva et al., 2019).

Thus, studies of the taphonomic process on the basis of ornithogenic material taking place in real time provide new results, both in terms of accumulation characteristics and subsequent modification of animal remains. The information obtained makes it possible to more determine accurately the bias of data from localities from the characteristics of communities in nature.

INITIAL STAGES OF THE TAPHONOMIC PROCESS

Biological factors of sediment averaging over a number of years. There are a number of factors that do not allow direct use of the results of analysis of the composition and structure of small-mammal remains from multilayer sediments to reconstruct the interannual dynamics of their abundance. Using mathematical modeling, it was shown that the maximum time for averaging the stable state of communities in ornithogenic localities is 140 years, and the relative abundance in communities and in sediments on the scale of centuries differs only slightly (Terry, 2008). The discrepancy value varies significantly in different types of sediments. In a large number of long-term neontological studies of bird nutrition, it was shown that their diet contains information both on the short-term cycles and the outbreaks of abundance of individual species and on the long-term trends in populations of small mammals (Love et al., 2000; Sadykova and Smirnov, 2005; Terry, 2009; Lyman, 2012; Milana et al., 2018). The dynamics of the representation of the major, alternative, and accompanying prey in the diet of owls in sediments is averaged over a number of years. In ornithogenic localities, the major prey items of owls accumulating the material are dominant; alternative prey items also account for a considerable proportion of remains due to an increase in their number in the diet of birds in certain years (Korpimäki and Sulkava, 1987; Sadykova and Smirnov, 2005). The accompanying prey items account for a few percent. The accumulation of pellets is uneven in different years. These patterns should be borne in mind when studying sediments, because they largely explain the ratios of the proportion of different species. The combination of data of long-term monitoring of the bird diet and the state of small-mammal communities with an analysis of sediments that were formed in the same time period provide information on the scale of events recorded in the chronicle of ornithogenic sediments. On the basis of studies on the long-term dynamics of animal abundance performed by Okulova (2009), four types of periods were identified: microdynamics (up to 10–12 years), mesodynamics (tens of years), macrodynamics (hundreds of years), and mega-dynamics (thousands of years or more). It was shown that the first two types are characterized by cyclical fluctuations in abundance; for the more extended periods, long-term trends can be distinguished. To perform a study at the intersection of neontology and paleontology, it was proposed to use terminology based on the degree of transformation of the composition of the fauna and the structure of communities rather than on the chronological measures (Smirnov and Sadykova, 2003). In accordance with this approach, the dynamics is subdivided into three scales: actual, historical, and evolutionary. On the first scale, fluctuations in the relative abundance of species occur, which do not lead to stable trends in the change of dominants and fauna composition. On the historical scale, the dynamics acquire stable trends of changes in the fauna composition and in the population structure. On the evolutionary scale, transformations of zonal groups and dominant species take place. The scale of the dynamics of the fauna composition and the population structure can be estimated on the basis of series of reconstructions that would allow proceeding to the description of processes at the level of the corresponding regions rather than on the basis of materials obtained from single locations. Bearing in mind the development of a multiscale approach to the problems of landscape science and other branches of geographical sciences (Khoroshev, 2016), the prospect of combining this approach with an analysis of the temporal dynamics of ecosystems on the historical and evolutionary scales should be considered.

Transformation and loss of morphological data at the initial stages of fossilization. Recently, taphonomic studies of the transition of organic matter from the biosphere to the geological record have been significantly developed. Especially notable advances were made in studies devoted to the actualistic investigation of modern processes through observations, experiments, and modeling and their application to the problems encountered in the studies of fossil material. Research in this field is based on comparisons of buried and modern bones, experimental placement of animal remains under conditions of existing localities for a long time, and experimental laboratory work (Andrews, 1995; Denys, 2002; Fernández-Jalvo and Andrews, 2003; Smoke and Stahl, 2004; Terry, 2004).

A series of studies showed how pellets in places of their accumulation undergo degradation under the influence of invertebrates, bacteria, fungi, water, and temperature (Levinson, 1982; Andrews 1990, 1995; Fernández-Jalvo et al., 2002; Terry, 2004). Then, if bone remains are covered by sediments, they are influenced by the factors that depend on the type of host rock (acids, alkalis, and water), as well as by a complex of biotic factors. Bone remains are mechanically affected by particles of different sizes that make up the sediments. The taphonomic modification of the microrelief of the occlusal surface of the teeth was estimated. It was shown that it can be easily identified and causes obliteration rather than a secondary change in characters (King et al., 1999). The preservation of the bone material from pellets when they are squeezed in sediments with different sizes of constituent particles was evaluated experimentally. It was shown the damage to bones buried among smaller particles is greater than in a larger pebble-gravel sediment (Smoke and Stahl, 2004). An experimental study showed differences between the surfaces of bones subjected to acid erosion and abrasion (Fernández-Jalvo et al., 2014). Abrasion of bone residues under the influence of water transport was studied (Fernández-Jalvo and Andrews, 2003). The results of the impact of various factors on bone remains and teeth during the taphonomic process are illustrated in the summarizing work (Fernandez-Jalvo and Andrews, 2016).

Sedimentation and other geological processes associated with the formation of the fossil record based on pellet material. The typology of accumulations of bone remains of the prey of eagle owls in karst cavities in the Urals was performed on the basis of analysis of sediments in more than 50 localities. Sediment accumulation in such caves may proceed in three ways. The least amount of accumulation occurs autochthonously and due solely to one agent—rock weathering. Under such conditions, bone remains are in the rubble in a carbonate environment and are covered with a calcite crust or "flour," which create a good environment for preservation of the bone tissue. Significantly more loose sediments accumulate in sheds and grottoes when soil is formed here and plant litter accumulates. In such an environment, bone remains undergo biological degradation, which is poorly compensated for by fossilization. The third type of sedimentation combines several sources of mineral particles, the main ones of which are the products of chemical weathering of carbonates in the form of loams; these products are removed from the interior of the cavity.

The osteological component may occupy different places in the sediment composition. For example, in Bol'shoi Glukhoi and Dyrovatyi Kamen' grottoes on the Serga River, horizons that did not contain anything except the bone remains of rodents and birds were found (Smirnov, 1993). This abundance was created without sorting by size or any other criterion. It is important to evaluate how the fossil record is distorted in aggregations of different types as a result of various lithological and taphonomic processes. Let us mention the most important of them.

The accumulation of both pellets and their host rocks may proceed unevenly on different time intervals, even within a seemingly homogeneous rock mass within the same location. In a number of cases, this unevenness can be detected only by using a series of radiocarbon datings. For example, in the Sukhorechenskii Grotto, accumulations of bone remains of the prey of an eagle owl were uncovered in a 35-cm thick rock. The lower part of the sediments was 1478 ± 211 years BC, and the upper part was in the interval between 1682 and 1735 AD. Due to the presence of 12 datings between them, a break in sedimentation with a duration of 500 years was found, which significantly changes the idea of the fauna structure dynamics for such a section (Smirnov et al., 1992).

Burial of the bones of prey and their transformation into subfossil remains may be accompanied by their partial loss. This process is always selective in at least two aspects. First, due to the different resistance of different skeletal elements to destruction, and second, due to the different strength of the same elements in different species. Selective loss of various bone remains at the stages of their collection and washing is also possible. The specific mechanism of sorting bone remains of small mammals in some karst cavities is worth particular mention. This applies to small objects in ornithogenic accumulations occurring in rubble sediments not consolidated by finely dispersed rocks. Small teeth of rodents fall out of the alveoli of the jaws; they spill through crushed stone much faster than the large teeth and do not fall into the collection when the upper horizons of sediments are excavated. This creates a peculiar "rubble sieve" phenomenon, which brings selective and marked transformations to the collections. In the literature, methods for assessing the preservation of the remains in relative values and in points have been proposed (Smirnov et al., 1986). The selection of the indicator is determined by the purpose of the work.

The formation of sediments may be accompanied by the movement of bone remains; as a result, the correct stratigraphic sequence is disrupted. Young remains may move into older layers, and vice versa. Identification of such redepositions would be an easy task provided the development of simple and inexpensive methods for dating small bone samples. Since such methods are still absent, researchers have to use the estimates of the degree of homogeneity of presumably synchronous bone remains based on indirect characters. Such estimates can be provided by a combination of thermogravimetry with an analysis of the accumulation of rare earth elements (Smirnov et al., 2009). This combination takes into account the multidirectional trends (the loss of organic matter and the accumulation of rare earth elements).

CONCLUSIONS

The direction of research to which this paper is devoted has been developed significantly in recent decades. In the second half of the 20th century, its foundations were created in Russian scientific schools under the leadership of I.M. Gromov, L.G. Dinesman, and A.K. Agadzhanyan. A qualitatively new stage in this direction was marked by the publication of the monograph *Caves, Owls,* and *Fossils* by Peter Andrews (Andrews, 1990). This work filled a significant gap in studies of the taphonomy of small mammals, which until then had been developed mainly on archaeozoological material (Lyman, 1994). The foundation of the specialized periodical *Journal of Taphonomy* had a noticeable positive influence on the development of this topic. Analysis of the published data mentioned above showed the achievements of a number of teams and individual researchers from Great Britain (P. Andrews), Spain (Y. Fernández-Jalvo), the United States (L. Lyman and R. Terry), Israel (O. Comay and T. Dayan), and Lithuania (L. Balčiauskas and L. Balčiauskienė). The studies involve extensive data on the growth and development of animals, the peculiarities of the foraging behavior of owls, and the predator–prey problem. An important condition for obtaining new results is the use of high-tech methods such as the analysis of stable isotopes, trace element composition of bone remains, electron microscopy, and 3D scanning of dental microsurfaces, as well as mathematical modeling of the dynamic processes of the past to predict the future. A characteristic and important feature of the development of this direction is the combination of analytical and experimental approaches for modeling the transition of living organisms into a subfossil state.

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COMPLIANCE WITH ETHICAL STANDARDS

The authors declare that they have no conflict of interest. This article does not contain any studies involving animals or human participants performed by any of the authors.

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