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Main and Concomitant Prey of the Eagle Owl (*Bubo bubo*) in Problems of Historical Ecology

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Abstract—This paper considers mass materials related to the feeding of the eagle owl from three latitudinal regions of the Urals (northern and southern taiga and steppe). All collections were carried out in the same type of location of bone remains of prey from pellets at the nesting grounds of eagle owls in niches and caves at cliffs along riverbanks. The prey of the eagle owl is divided into three categories: main, alternative, and concomitant. The paper shows the degree of correspondence of the proportions of individuals of different species and their groups in the diet of the eagle owl and the population of rodents in the environs of nesting areas. The importance of separate consideration of the main and other prey of the eagle owl in reconstruction of the composition of the fauna and structure of the rodent population based on subfossil ornithogenic materials is emphasized.

Keywords: eagle owl nutrition, pellets, rodents, subfossil remains, community reconstruction, Holocene, taiga, steppe

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INTRODUCTION

Historical ecology, or the history of biogeocenoses in the Holocene, has been intensively developed in recent decades based on the foundations laid in Russian science thanks to the scientific schools of V.N. Sukachev, L.G. Dinesman, and I.M. Gromov. A particularly important role in this development was played by the Laboratory of Historical Ecology, which was founded at the A.N. Severtsov Institute of Evolutional Morphology and Ecology of Animals of the Soviet Academy of Sciences by L.G. Dinesman, who would have turned 100 years old in 2019.

The basis for the solution of a number of problems of historical ecology is information on the mass accumulations of bone remains of small mammals, which formed as a result of the feeding of predatory birds. The eagle owl (*Bubo bubo* Linnaeus, 1758) was one of the main accumulators of such material as early as a few decades ago in several regions, in particular, in the Urals. The nests and sitting places of this predator were located in remote places on the rocky banks of rivers in shelters and caves. There, mixing with the products of physical and chemical destruction of karsting rocks, bones from pellets undergo the initial fossilization stages and form bone-bearing horizons [1, 2]. The widespread decrease in the numbers of the eagle owl has quickly made these sources of subfossil material increasingly rare, but once-inhabited nests are still available for study by paleontological methods.

The feeding habits of the eagle owl have been considered in the ornithological literature from different standpoints and in great detail [3–5]. Having a vast range with a huge variety of habitat conditions and a wide range of potential prey, this species is classified as a universal predator due to the diversity of its food. It is noted in some special cases that the eagle owl is not "distracted" by various prey when there is abundant attractive and easily accessible prey of one particular species [6]. This situation is not frequent. As a rule, eagle owls hunt in a territory such that almost all rodent species of suitable sizes are among their prey within several years [3–5, 7]. In addition, the food range of these predators includes birds, but their analysis is beyond the scope of this study.

This paper will focus on the part of the list of prey that does not usually attract the attention of ornithologists. Our tasks include a comparative analysis of not only the main, but also the concomitant, prey of eagle owls from different latitudinal regions of the Urals. It includes species that by no means comprise the main proportion in mass. Predators get concomitant prey not only in hunting areas, but also in transit territories. It is these species that serve as indicators of whether the surrounding landscape includes habitats that are important for paleoreconstructions but are secondary to the foraging activity of predators.

MATERIALS AND METHODS

This paper is based on published material collected from different latitudinal regions of the Urals: the northern taiga of the Pechora-Ilychsky Reserve [8], the southern taiga at the border with the forest steppe in the Middle Urals [9], and the steppe of the southern extremity of the Ural Range [10]. The bone-bearing layers in each of the studied nests have different thickness and accumulated over a particular chronological interval within the Holocene. Eagle owls periodically continue to nest in some of them at present. The information that some nests belonged to eagle owls some time ago was obtained from workers at the environmental protection structures of the corresponding territories. Some nests and sitting places do not bear traces of recent nesting, but these places could not be inhabited by other predators. The surface part of sediments in such shelters and caves contains some amount of bone remains of small animals with obvious signs of excretory origin [11, 12]. After the soil is washed out, shell fragments of eagle owl eggs are found in it. Excavations and cameral processing of osteological materials were carried out according to the standard paleontologic techniques. The number of preyed individuals was estimated based on bone remains of the same type (teeth).

The attribution of the species to the main or concomitant prey was carried out based on the proportion of individuals of the corresponding species in the prey. There may be no strict quantitative boundary between main, alternative, and concomitant prey, since this is a mobile characteristic that is determined by the structure of the dominance of victims in the diet. The prey categories are distinguished via analysis of the nutrition of the predator for a number of years, which includes different phases of prey-abundance dynamics [13, 14]. Information of this type cannot be obtained from analysis of subfossil and fossil material, since this material consists of prey remains that have accumulated over dozens or hundreds of years.

Based on comparative data on recent materials [3–7], we consider that the species dominant in ornithogenic sediments are the main prey. The majority of the prey list is made up by concomitant prey, but the share that is accounted for by each of these species is insignificant. It is most difficult to distinguish alternative prey in ornithogenic material that accumulated over a long period of time, since these species periodically reach a significant share of the diet. The number of such victims in the average diet is intermediate between the main and concomitant prey. The mass of prey was calculated according to the data given for rodents in reference books and field guides [15].

RESULTS AND DISCUSSION

The main prey is different in each of the latitudinal regions of the Urals depending on the habitats in which the predator catches the prey. In the taiga conditions of the upper reaches of the Pechora River, these are usually floodplain meadows, where the main prey is the water vole. If the meadow area is small, eagle owls obtain squirrels in forest areas (parmas) (Fig. 1). The mass proportion of these species in floodplain habitats is 50 and 36%, respectively; in parmas, it is 14 and 65%. Regardless of the main prey, the list of eagle owl prey includes almost all terrestrial rodent species that have suitable sizes as prey. The proportion of each of them by the number of caught individuals varies from single digits units to 10%, and their mass proportion is significantly less. In total, the remaining nine prey types account for 50% of individuals and 18% of the mass (on average 6 and 2% per each species, respectively). The species list gives a clear idea of the fauna in the region: inhabitants of forest and near-water habitats. According to capture data [16], the core of the rodent community in this region is made up by the northern red-backed vole and bank vole—these are numerous species with relatively stable abundance dynamics. In the years of an increase in the abundance of small mammals, there are high numbers of the field vole, tundra vole, and wood lemming; in the years of depression, they are almost completely absent [16]. The species that form the basis of the rodent community according to capture data (northern red-backed vole and bank vole) both accounted for 5% on average of the eagle owl's prey and must be classified as concomitant prey. Significant fluctuations in the numbers of tundra vole and wood lemming and relatively high proportions of these species in the eagle-owl diet suggest that they can play the role of alternative prey. The grey-sided vole probably belongs to the same category.

In the Middle Urals, the main prey of the eagle owl in terms of the number of caught individuals includes two species: the water vole and the common vole (Fig. 2). The first species (a floodplain inhabitant) sharply prevailed in the prey of inhabitants of the Bazhukovo shelter; the second species in terms of the proportion of caught individuals was the common vole, which inhabits meadows and farmlands. In the Sukhorechensky grotto, the proportion of these species was the opposite. This is easily explained by the difference in the habitats surrounding the nests. In the immediate vicinity of the Sukhorechensky grotto, in addition to the Serga River floodplain, there are vast spaces of fields and lands for various agricultural uses in the Krasnoufimsky forest-steppe. Here the population of small rodents is dominated by the common vole. On the other side of the river, there is the Ufimskoe Plateau, which is covered with southern taiga forests. The common hamster has the greatest proportion of mass in the eagle-owl prey in the Sukhorechensky grotto (55%), but the water vole also makes up a significant proportion of the mass (30%). The latter is absolutely dominant among the prey of inhabitants of Bazhukovo shelter (76%). For the remaining victims (11 taxa), the proportion of caught individuals is 19% in these places

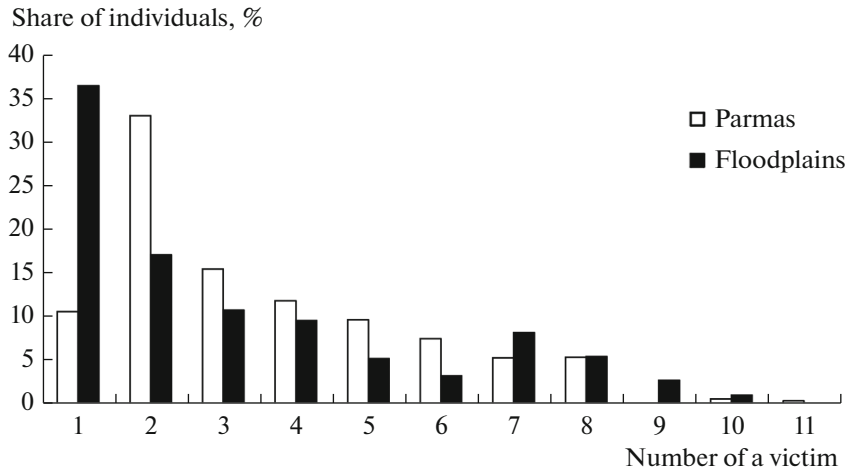

Fig. 1. Shares of individuals in the eagle-owl diet in the Pechora River floodplain and in the taiga areas (parmas) of the Pechora-Ilychsky Reserve (Northern Urals) according to [8]: 1—*Arvicola terrestris*, 2—*Sciurus vulgaris*, 3—*Microtus oeconomus*, 4—*Clethrionomys rufocanus*, 5—*Myopus schisticolor*, 6—*M. agrestis*, 7—*Cl. glareolus*, 8—*Cl. rutilus*, 9—*Pteromys volans*, 10—*Eutamias sibiricus*, 11—*Ondatra zibetica*.

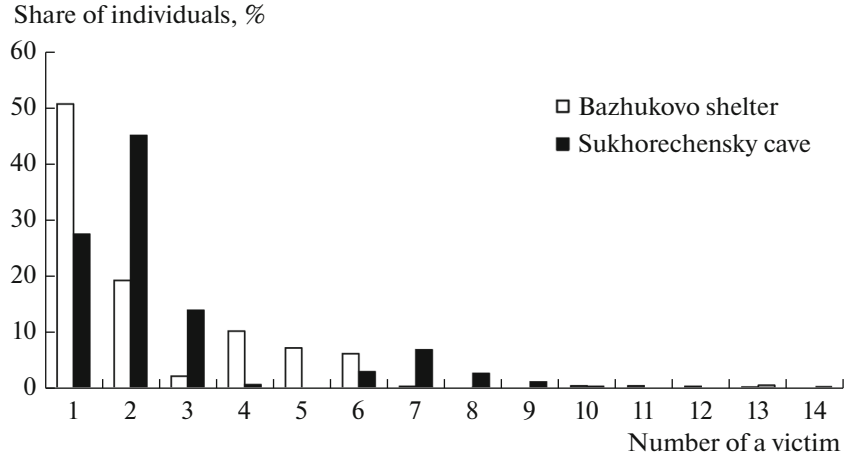

Fig. 2. Shares of preyed individuals in the eagle-owl diet in the Middle Urals according to [9]: 1—*A. terrestris*, 2—*M.* ex gr. *arvalis*, 3—*Cricetus cricetus*, 4—*M. oeconomus*, 5—*Clethrionomys* sp., 6—*M. agrestis*, 7—*Apodemus* sp., 8—*Cl. glareolus*, 9—*Cl. rufocanus*, 10—*Sciurus vulgaris*, 11—*Sicista betulina*, 12—*M. schisticolor*, 13—*P. volans*, 14—*Rattus norvegicus*.

and the mass proportion is 5.5% (on average, 2 and 0.5% per each species, respectively).

The capture of rodents with live traps and cones in various habitats of the Serga River floodplain showed [17] that it was dominated by the bank vole and tundra vole. If we calculate the average proportions of the main species in eight habitats in which rodents were caught with different tools, then their sequence in descending order will be as follows: bank vole (38%), tundra vole (20%), pygmy wood mouse (11%), northern birch mouse (9%), and field vole (8%). Of course, the results of one-time captures are difficult to compare with multiyear data on the eagle owl prey, but the presented materials give a satisfactory idea of the population of floodplain areas. These data can be compared with the data on the Bazhukovo shelter. The species' compositions in these samples coincide, with the exception of those rodents that could not be caught by live traps and cones but were preyed upon by the eagle owl. A special place in the captures is occupied by the bank vole, which is dominant in these areas. It accounted for only a few percent in the eagle-owl prey and undoubtedly must be assigned to the category of concomitant prey, like ten other species with small proportions of prey individuals. The only species that occupied a significant place in the eagle-owl diet (10%) was the tundra vole. This gives grounds to consider it an alternative prey. This assumption is not contradicted by the significant proportion of the tundra vole in the captures.

In the Verblyuzhka 1 and Verblyuzhka 2 grottoes in the steppes of the southern extremity of the Urals, the

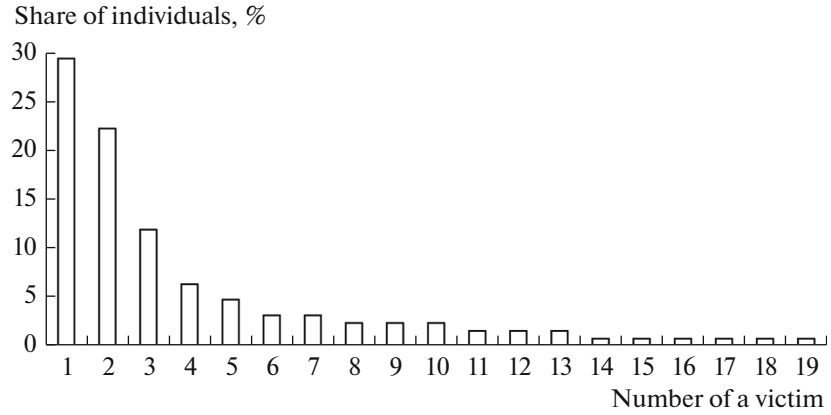

Fig. 3. Shares of preyed individuals in the eagle-owl diet in the Southern Urals according to [10]: 1—*Ellobius talpinus,* 2—*Cricetus cricetus,* 3—*M.* ex gr. *arvalis,* 4—*Ochotona pusilla,* 5—*A. terrestris,* 6—*Allactaga major,*7—*Clethrionomys rutilus,* 8—*Allocricetulus eversmanni, 9—M. gregalis,* 10—*Mus musculus,* 11—*A.* ex gr. *uralensis-agrarius,* 12—*Cl. glareolus*, 13—*Cricetulus migratorius,* 14—*M. agrestis*, 15—*Sylvaemus uralensis,* 16—*Rattus* sp., 17—*Spermophilus* cf. *pygmaeus,* 18—*Sicista* sp., 19—*Dipus* sp.

main proportion of the eagle-owl prey by the number of individuals is comprised of the northern mole vole, common hamster, and common vole (Fig. 3), but the hamster is strongly prevalent in mass (71%). The proportion of the remaining 16 species in terms of the number of preyed individuals is 36%, and their mass proportion is 22% (on average 2 and 1% per each species, respectively). The natural population of small mammals underwent a deep anthropogenic transformation after the development of virgin and fallow lands in the middle of the 20th century [18]. Where agrolandscapes prevail, the communities of small mammals are everywhere dominated by the common vole. The mass species in floodplains with tree-shrub vegetation is the bank vole [19, 20].

There continue to be significant changes in the population structure of small mammals in recent decades. Unfortunately, we have not managed to collect recent material from sediments of the Verblyuzhka grotto for a reliable comparison with the average eagle-owl diet. It can be used for comparison with the main and concomitant prey from other regions of the Urals. Such a comparison shows the zonal features of the eagle-owl prey in steppe, floodplain, and other habitats, which are a good reflection of the current stage of the development of regional rodent communities [10].

CONCLUSIONS

1. In all latitudinal regions of the Urals, the composition of the eagle-owl prey perfectly reflects the composition of the rodent fauna.

2. The main eagle-owl prey may belong to zonal complexes or groups of other categories. In the northern taiga, southern taiga, and steppes, the main eagle-owl prey was revealed to include the following rodents, respectively: squirrel and water vole; common vole, water vole, and common hamster; northern mole vole, common hamster. In terms of the proportion of preyed individuals, the main prey on average accounts for 48, 70, and 52% in the Northern, Middle, and Southern Urals, respectively. The northern taiga is the only region in which the main eagle-owl prey includes an inhabitant of forest habitats—the squirrel. All other main preyed species live in open and near-water habitats, and their composition reflects the preferences of the eagle owl in the chosen hunting areas.

3. The list of concomitant prey of the corresponding regions includes the following number of species: 9 (northern taiga), 12 (southern taiga), and 16 (steppe). The proportions of individuals are reflected in the structure of the concomitant eagle-owl prey selectively in accordance with the frequency of predator visits to the corresponding habitat rather than in proportion to their abundance in nature. There may be situations in which a species from the list of concomitant prey is dominant in the rodent community.

4. In order to solve the problems of historical ecology in the reconstruction of the composition of the fauna and structure of the population of small mammals based on subfossil materials from accumulations of eagle-owl pellets, it is necessary to consider the main and concomitant prey separately. If the main prey includes species from zonal complexes, their characteristic is decisive. If the main prey does not include species from zonal complexes, the reconstruction may be based on the list of concomitant prey, which takes into account the selectivity of their prey.

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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 performed by the authors.

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