Zoodiversity, **54**(5): 419–432, 2020
DOI 10.15407/zoo2020.05.419

Ornithology

UDK 298.279:57.022:57.017.3

SPATIAL AND TEMPORAL CHANGES IN FALCONIFORMES AND STRIGIFORMES NUTRITION: CAUSES, SIGNIFICANCE, CONSEQUENCES

I. Komarnytskyi, I. Shydlovskyy, I. Zahorodnyi

Ivan Franko National University of Lviv,
Hrushevskogo st., 4, Lviv, 79005 Ukraine
E-mail: shydlyk@gmail.com; vaniazahorodniy@gmail.com

I. Komarnytskyy (https://orcid.org/0000-0002-8720-0552)
I. Shydlovskyy (https://orcid.org/0000-0002-1003-2562)
I. Zahorodnyi (https://orcid.org/0000-0003-2621-4202)

Spatial and Temporal Changes in Falconiformes and Strigiformes Nutrition: Causes, Significance, Consequences. Komarnytskyi, I., Shydlovskyy, I., Zahorodnyi, I. — Spatial and temporal changes in the nutrition of four species of diurnal birds of prey and six species of owls, traditionally referred to polyphages (generalists), are considered. Based on the literature data and our own observations, we have provided a classification of birds of prey according to their feeding and nest building characteristics. The main ways of interaction of these aspects of raptors life and the importance of their understanding for the effective planning and development of measures for the conservation of the studied species are presented.
Key words: nutrition factors, trophic relationships, birds of prey, Falconiformes, Strigiformes, polyphages (generalists).

Introduction

Nutrition is one of the factors that affect all aspects of animal ecology and ethology the most (biotopic distribution, territorial behavior, migration, fertility, and population dynamics) (Novikov, 2001). The fullness of the trophic spectrum is an indicator of the species' ability to adapt to changes in food reserves (Galushin, 2005). According to the spectra of nutrition among falcons, as well as among other consumptions, there are: monophages (feeding on one kind of victims), oligophages (several types of victims) and polyphages (opportunists feeding on many kinds of victims). Such separation is rather conditional, since even monophages under a sharp decrease in the number of the main species of the victim exhibit plasticity in nutrition (Novikov, 2001). In spite of this fact, the numbers of monophages and oligophages are more dependent on the number of their major feeding target compared to polyphages (Terraube et al., 2010), whereas the relatively stable number of polyphages depends on the ability to change their diet in response to different types of victims (functional response)

(Galushin, 2005; Terraube, Arroyo, 2011). In this case, particular attention is paid to studies aimed at identifying mechanisms for the adaptation of birds of prey to the spatial and temporal change in the composition of victims in nature (Zuberogoitia et al., 2006), because of population stability of predators is ensured in two ways:

1) alteration of trophic communications on the permanent territory;

2) alteration of spatial relationships in search of constant (stereotyped) food (Galushin, 2005).

The subject of analysis in this work is changes in the birds of prey nutrition, aimed at their adaptation to variable environmental conditions. We selected four falcon species as the object of analysis — the Montagu's Harrier, *Circus pygargus* (Linnaeus, 1758), the Common Buzzard, *Buteo buteo* (Linnaeus, 1758), the Lesser Spotted Eagle, *Aquila pomarina* C. L. Brehm, 1831, the Common Kestrel, *Falco tinnunculus* Linnaeus, 1758, and six species of Strigiformes — the Eurasian Eagle-Owl, *Bubo bubo* (Linnaeus, 1758), the Long-Eared Owl, *Asio otus* (Linnaeus, 1758), the Little Owl, *Athene noctua* (Scopoli, 1769), the Eurasian Pygmy Owl, *Glaucidium passerinum* (Linnaeus, 1758), the Tawny Owl, *Strix aluco* Linnaeus, 1758, and the Western Barn Owl, *Tyto alba* (Scopoli, 1769), considered as polyphages (generalists). Compared to monophages and oligophages (specialists), their food spectrum varies widely depending on the specific environmental conditions. Owls are ecologically the nocturnal counterparts to diurnal birds of prey, without being related to them. This phenomenon in biology, in which unrelated groups come to resemble each other through adaptation to similar lifestyles, is called convergence. It is found in a considerable diversity of animal and plant groups. Anatomically and behaviourally there are large differences between such groups although they occupy similar ecological niches (König, Weick, 2008). The aim of this work was to analyze changes in the birds of prey feeding under the influence of all possible factors within specific spatial and temporal frameworks.

Nutrition — a key factor in the life of birds of prey

Almost whole activity of bird, including falconiformes and owls, can be directed to finding food with the exception of the breeding season (Elkins, 2004). We can conclude from this statement that the nutrition has exceptional value for birds. The role of the trophic factor in the life of birds of prey can be estimated by its influence on the population size — "a generalized indicator of the viability of any species, a starting point for the full characterization of the effectiveness of ecological connections and adaptive strategies" (Galushin, 2005). However, it is extremely difficult to estimate such an impact because of the indirect effect of the trophic factor on population dynamics, which depends on such processes as fertility, mortality, immigration and emigration (Tsaryk, 2005). Let us briefly consider the influence of the trophic factor, separately, on each of these processes in the life of birds of prey.

"Fertility" is defined as the number of individuals born over a period of time (Tsaryk, 2005), and therefore for birds, "fertility" depends on the quality of the eggs (size, nutrient content) and the number of eggs in the nest. Thus, prenatal development and the size of the chicks depend on the size of the eggs and their nutrient content. The size and energy value of eggs are positively correlated with the activity of the metabolism of the female during egg formation, which depends on the quality of its nutrition. In addition, it is known that with increasing egg size of the Common Kestrel the probability of hatching of all chicks in the nest increases (Valkama et al., 2002). It has been established that in the years of large populations of voles, laying of Montagu's Harrier appeares faster and their average size is larger (Koks et al., 2007). We can observe the same feature in the barn owl (König, Weick, 2008; Bernard et al., 2010; Paspali et al., 2013). According to our observations a significant number of eggs and chicks were in the nests of the Western Marsh Harrier, *Circus aeruginosus*, the Long-Eared Owl, and the Northern Goshawk, *Accipiter gentilis* (Linnaeus, 1758), in 1988 and 1998 on the territory the Shatsk National Nature Park and its buffer zone, including 5 in each of the first two species and 4 in the Northern Goshawk. And in 1998 a clutch of 5 eggs was found in the Eurasian Sparrowhawk, *Accipiter nisus* (Linnaeus, 1758). In other years, in particular until 2010, we observed a smaller number of eggs in the clutches of these species of birds of prey — 2–3, in the barn owl — 4.

Interestingly, even the sex ratio of birds of prey depends on the availability of feed. For example, in Estonia, in years with a lack of fodder resources, the number of males among chicks of Lesser Spotted Eagle exceeded the number of females, in contrast to years when there was much food (Väli, 2004). The same sex ratio, which depends on the deficiency or abundance of voles, is also typical for the brood of Common Kestrel in Finland (Korpimäki et al., 2000). Scientists attribute this phenomenon to the fact that in years, which are poor for feed, it is more difficult to feed energy-intensive females in the brood, and determining a sex in chicks occurs when laying eggs. The sex of the chicks is influenced by the hormonal background of the female, which obviously depends on the presence of nutriment.

Mortality. The direct lethal impact of the trophic factor on birds of prey is a rare fact, since they can live without food for a long time. However, prolonged adverse weather conditions can complicate or even make hunting impossible, leading to the exhaustion and even death of birds, which is often observed in winter. For example, in the winter of 1962/63 in Transcarpathia, there were significant deaths rate of Barn Owls and other wintering birds due to severe weather conditions (the air temperature dropped to –30 °C, which is not typical for the region). Adverse weather may make it difficult for parents to access food, or it may increase feeding needs for chicks and lead to increase their mortality. Due to lack of food, birds become weak and ill or fall prey to predators, what hides the main cause of death from researchers. The phenomenon of "Cainism" (manifestation of cannibalism) deserves special attention (Meyburg et al., 2008). Its point is that the older and, therefore

stronger, chicks eat the younger. The important biological significance of this manifestation of behavior is determined by the fact that one healthy chick survives better for the population than two feeble birds. This is predominantly characteristic of eagles, in particular, most pronounced in the Lesser Spotted Eagle and the Northern Goshawk, but it can be manifested in other representatives of Falconiformes in case of acute insufficiency of the feed. We observed this phenomenon in the nests of Kestrels in 2017–2018. Usually, the first is eaten a chick, which hatched last, and for 1–2 weeks of life. However, there was a case in Lviv in 2018 when the elders had eaten a 4-week-old chick.

We observed the nest of the Northern Goshawk from the beginning of egg-laying to the departure of chicks near the village Polapy of Lyuboml District, Volyn Region in 1988. Only two chicks flew out of the clutch, having 4 eggs. The other two had been eaten by the older ones: the first three two-week-old chicks had eaten the youngest and the smallest, and during the next week — another, which also lagged behind them in growth.

Thus, it was previously believed that "cannibalism" of the lesser spotted eagle manifests itself in all nesting cases and, accordingly, the only one chick always leaves the nest. However, recent studies indicate that even for the Lesser Spotted Eagle, this phenomenon depends on the food supply, since in the years, when the number of voles was high, birds feed two chicks successfully (Väli, 2012).

In the study of birds of prey, the most commonly used is the integral index, which includes fertility and mortality in breeding, namely breeding success (the number of young birds that successfully left the nest during the breeding period) (Gavrilyuk, 2009). For example, in Spain, the efficiency of nesting of the Montagu's Harrier correlates with the number of the Granada Hare, *Lepus granatensis* (Rosenhauer, 1856), despite the fact that the Harrier eats a variety of fodder (Arroyo, 2006).

However, the productivity of nesting of birds of prey is limited by food even in years with a high number of major victims. This was proven by data from a long-term experiment with Kestrels, during which one dead mouse was added daily in the experimental nests. As a result, the productivity of nesting was higher in the study group than in the control group, compared to years with low and high numbers of voles. For example, such factor as weather influences productivity of nesting of Falconiformes and Strigiformes indirectly through food. In particular, scientists have found that summer rainfall is adversely effects on breeding of the Common Buzzard, which is associated with a negative impact on the density of small rodents (Krüger, 2004). This is also confirmed by our observations of breeding the Long-Eared Owls in 2019 within the Buchach District of Ternopil Region. Prolonged rains that lasted almost continuously for two weeks resulted in 40–50 % mortality of chicks that reached 4 weeks of age and a significant weakening of those who survived. In comparison, the masonry was the same in the same region in the previous year, but mortality among chicks was 7–10 %.

However, in some cases rainfall may have a positive effect on reproduction. For example, the productivity of the Lesser Spotted Eagles correlates positively with the presence of rains in April and July, which is associated with the massive reproduction of amphibians in the previous year (Väli, 2012).

Immigration and emigration. The term "migration" for birds means regular flights: in spring — to permanent nesting places, in autumn — to permanent places where they spend pass the winter (Newton, 2008). Therefore, the term "immigration" and "emigration", which means the movement of individuals for long-term or permanent residence, we denoted in this article by the term "resettlement" or "dispersal", where immigration — the settlement of a certain territory, emigration — eviction from a certain territory. Basically, all types of movement of birds of prey in space are associated with seasonal variations in food availability and directed at balancing predator numbers and the number of victims and finding new nesting areas (Galushin, 2005). Thus, in most of its habitat area, the Lesser Spotted Eagle chooses place to nest near reservoirs and reclamation systems (Mykytyuk, 2000), where the number of amphibians is highest (Väli, 2004). However, for example, in Slovakia, where Spotted Eagle nest at altitudes of 325–800 m above sea level, the presence of wet meadows and swamps is not a limiting factor for their nesting. In this case, the availability of nutriment plays a major role. The key role of the trophic factor in the choice of nesting area may be confirmed by another case: the nesting of a Buzzard on a conventional rooftop of a semi-destroyed building at a height of 3 m above the ground in southeastern Spain and absence the forest nearby. This behaviour researchers explaine by the large number of the European Rabbit, *Oryctolagus cuniculus* (Linnaeus, 1758), in the surrounding area (Castillo-Góómez, Moreno-Rueda, 2011). Synanthropic species occur among owls, such as the Western Barn Owl, that have been nesting in human settlements for a long time. In the first half of the XXth century, the Western Barn Owl nested on the rooftops of tall buildings in the centre of Sofia and other major cities. Nowadays birds are practically not occure in large cities of Europe due to significant noise pollution (which significantly affects the success of hunting) and reduced availability of feed (Nankinov, 2002).

The density of birds of prey has been shown to depend on the presence of nutriment, but this connection is not direct:

1) the density of predators is higher in places where feed is available in sufficient quantities compared to places where feed is scarce (Butet et al., 2010; Sergio, 2005);

2) the density of predators is higher in years when feed is sufficient, compared to years when feed is scarce (Butet, Leroux, 2001);

3) long-term or cyclic changes in the density of predators are often accompanied by long-term or cyclical changes in the density of the main feed objects (Kokko, Ruxton, 2000; Lõhums, 2011; Reif et al., 2004).

4) the greater the variety of victims, the greater the variety of predators

Changes in nutrition as an adaptation. The term "adaptation" should be understood as special morphophysiological properties that ensure the survival and reproduction of organisms in specific environmental conditions (in our case, the interaction "predator-victim" in biogeocenosis). The potency of any adaptation is determined by environmental conditions, so adaptation is always relative to certain conditions (Yablokov, Yusufov, 2006). So, an adaptation of the Common Kestrel to see in the ultraviolet light spectrum is very important for hunting small rodents (Rodentia), and especially voles (*Microtus*). Poles mark their territory with scent marks (urine droplets) that absorb part of the ultraviolet spectrum and emit it in the form of visible light seen by Kestrel (Honkavaara et al., 2002). However, such adaptation will not help these birds to hunt rodents in the dark, instead of well-adapted owls (Strigiformes) (Aschwanden et al., 2005).

In owls the eyes are set frontally as in humans but their eyeballs are fixed. They cannot roll their eyes or move them in any way. Therefore they swivel their heads in order to see behind them. They can turn their heads through an arc of about 270°, thereby seeing backwards with great ease. The visual sense in owls is well developed. At dusk or in the very subdued light at night, owls are able to distinguish more details than the human eye, but even in bright daylight they can see perfectly. However, they are blind in total darkness (König, Weick, 2008).

Also, being active at dusk and at night, owls have highly developed hearing. This enables them to hear even the smallest rustling of prey in grass.

Some changes occur in the body under the influence of environmental factors. That can be accumulated by natural selection, then the organism will survive, or discarded and organism will die. Such changes include the adaptive behavior, but it is not inherited. However, the limits of modification variability (response rate) for each individual feature are fully determined by genotype (Dawkins, 2010). In other words, not the feature is inherited, but the norm of reaction to the influence of the environment (Yablokov, Yusufov, 2006). An example can be cited for birds of prey, that hunting a mammal that does not exceed the size of a wild rabbit is the norm for the Common Buzzard. This behavior of the Common Buzzard is related to the peculiarities of the body — relatively weak paws, low body weight, compared to, for example, a female the Northern Goshawk that can successfully hunt the Mountain Hare (*Lepus timidus* Linnaeus, 1758), which is about twice as heavy as a rabbit (Verdal, Selås, 2010).

Material and methods

The article based on our own observations and the study of literary sources about spatial and temporal changes in the feeding of birds of prey, aimed at their adaptation to changing environmental conditions. Four species of Falconiformes and six species of Strigiformes, common in Ukraine and traditionally considered polyphages, were selected as the object of analysis. We have studied sources since the mid-twentieth century and to nowadays.

Own researches were carried out during 2015–2019, in the territory of Western Ukraine in all available physical and geographical regions. We have analyzed the study area and created routes that would cover the nesting territories of the studied species as much as possible.

Phonograms were used to enhance voice activity of owls during accounting and searching for their nesting areas. The success of detection increases by 70–90 %, as observed in cases with Ural Owl, *Strix uralensis* Pallas, 1771 (Karyakin et al., 2000). We have played phonograms with different communication signals of all kinds of owls that can occur in certain area, starting with the smallest and ending with large species (Karyakin, 2004).

In addition, we used the method of pellets and forage residues analysis of birds of prey, which are widely used to study the spectrum of their nutrition. This method, to some extent, has replaced the analysis of the stomachs contents of birds, which requires the removal of animals from nature. The pellet analysis enables the study of trophic relationships between predators and their prey in different ecosystems (Atamas, 2004; Yatsjuk, 2008). We also used photo traps and made visual observations (through binoculars) of the hunting behavior of birds and identifying the objects of hunt.

Results and discussion

Factors affecting feeding of birds

Speaking of one particular case, in order for a predator to catch one particular feeding object, a whole chain of events must occur. First of all, the predator and the victim must meet in a certain place and at certain times and after the meeting the following events are possible:

Figure 1 shows very clearly that of the eight possible outcomes of the meeting, only one will lead to the death of the prey. Yes, many researchers give just such a correlation of successful and unsuccessful attacks of a predator. It be noted that for some birds, a successful

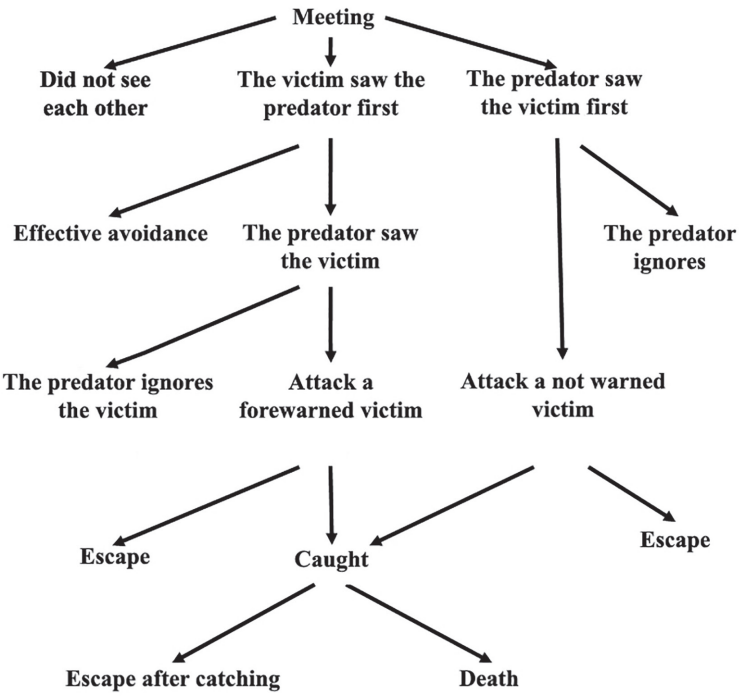

Fig. 1. Scheme of possible developments after the meeting of the predator and the victim.

attack does not necessarily end up eating prey. Some birds of prey, such as the Common Kestrel, stock up food (Rejt, 2006), since they can hunt even when not hungry. In some cases, these food reserve may be lost, which should also be considered in studies of these birds nutrition. The Boreal Owl *Aegolius funereus* (Linnaeus, 1758) is also characterized by the same behavior. The bird stores excess food in so-called pantries (in hollows, on branches, in bird nests), which are often important for survival in the winter. During the nesting season, it stores food near the nest. This behavior is less commonly observed for the Eurasian Pygmy Owl (König, Weick, 2008).

In general, the predator-victim interaction is a complex dynamic system that depends on the properties of the organisms that interact with each other and the factors of environment, where this interaction takes place. The factors affecting the victim should be separated — "prey factors" and predator factors — "predator factors". Moreover, different factors affect the different stages of their interaction (fig. 2). Therefore, in our opinion, it is useful to briefly describe each of these factors and pay attention to the most important of them. The characteristics are presented according the order of diagram shown in fig. 2.

Predator's factors

Seasonal changes in nutrition are due to factors such as weather (see below) and specific periods of predators' life (Novikov, 2001). The main periods are the nesting season, migration (nomadic life), winter hibernation, and the associated molting processes (or plumage condition that is closely related to flight properties). It is known that predators exhibit the greatest hunting activity during the nesting season, because during this period they have to feed themselves and the chicks. Bird nutrition has the greatest diversity in this period, the reasons for which will be discussed below. During the migration period, the feeding range of birds of prey alter due to changes in feeding areas and is naturally caused by seasonal changes in the lives of victims.

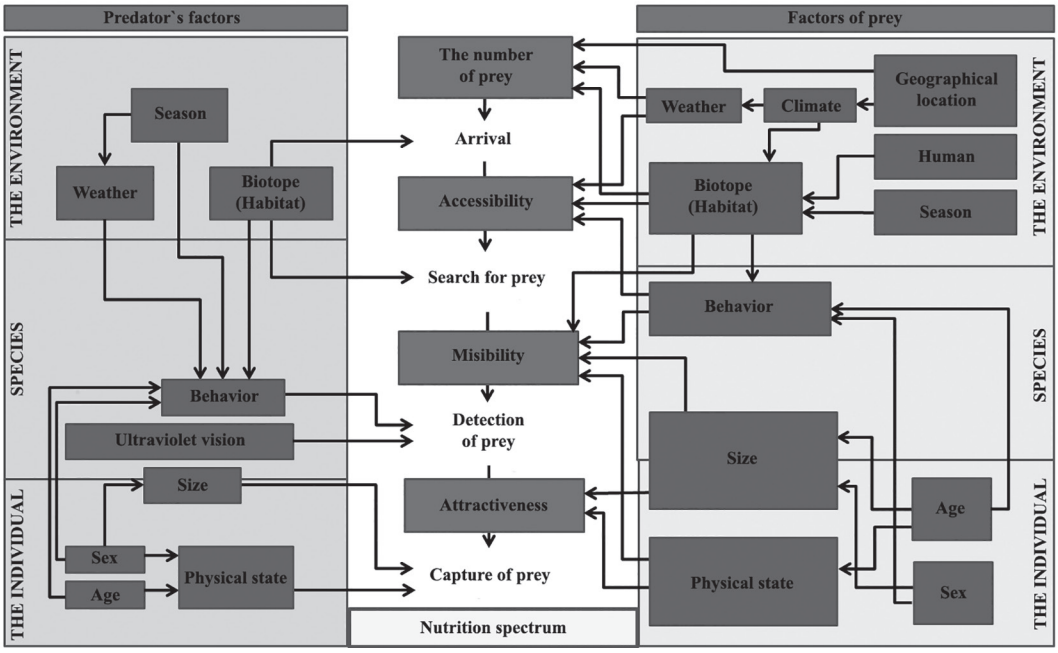

Fig. 2. Possible factors affecting the feeding range of birds of prey (according to: Birrer, 2009, as amended).

Weather is one of the most powerful factors that affect the activity of birds (Elkins, 2004), in particular it concerns owls and falcons (Galushin, 2005). First of all, it is worth noting air temperature, precipitation, air flows and fog among the weather factors. Thus, low air temperature accelerates heat output from the body of the bird, and therefore increases metabolism and increases energy expenditure on body heating (Elkins, 2004), especially for small predators. That is why in cold weather birds tend to "still-hunting", but they change hunting areas more often than during the warm season. Although the bird's flight generates enough heat to the body warming, this process also consumes a lot of energy on the wings waves (on the flight itself). In Utah (USA), it has been established that the American Kestrel, *Falco sparverius* (Linnaeus, 1758) decreases its activity already at 0 °C and below. In the Netherlands, it has been found that rain, fog, and wind speeds of more than 4–12 m/s greatly impede the hunting of the Common Kestrel in flight. It is worth mentioning such a unique feature as silent flight, which is directly related to the feather structure and is characteristic of most owls. This feature makes it possible to approach the victim unnoticed. However, the flight is much more complicated in the rain due to the considerable wetting of the plumage. The relatively rigid plumage that fits snugly to the body, like the Brown Hawk-Owl, *Ninox scutulata* (Raffles, 1822), have, characterizes the species that pursue rather than wait for their victims. The same applies to northern species (the Snowy Owl, *Bubo scandiacus* (Linnaeus, 1758) and the Northern Hawk-Owl, *Surnia ulula* (Linnaeus, 1758)), which are forced to hunt in the conditions of white nights and polar day.

The weather factors, such as low temperature and precipitation, combined to create the snow cover, a new powerful influence factor on the nutrition of birds of prey (Elkins, 2004). First of all, it affects predators that feed on terrestrial animals. Depending on the thickness of the snow cover, it may partially or completely block access to the main bird feed (Selås, 2001). Glaze formation further complicates the process of obtaining food (Żmihorski, 2007). Therefore, it is necessary to consider the season and weather conditions that preceded the collection of material. Such factor

concerned owls in a lesser extent, because they can find prey using only hearing. There are observations that Long-Eared Owls have detected and caught voles under 50 cm of snow cover. Similar facts are known about the Great Grey Owl, *Strix nebulosa* Forster, 1772, and the Ural Owl.

Biotope. Predatory bird-polyphages hunt in a wide variety of biotopes, beginning with the forest and ending with hunting above the surface of the water. Different biotopes are characteristic of different potential victims, so the search for prey depends on the type of biotope, and therefore the type of predator. The way of hunting also depends on the biotope. Yes, it is very important for many owls and falcons to have grafts on the ground, especially in adverse weather (Jenkins, 2000). Forest species of owls are tends to "still-hunting". It should be noted that the forest species of owls are hunted almost exclusively from the perch.

The behavior and adaptation of predator, most often closely related to victim`s behavior and adaptation (co-evolution) (Yablokov, Yusufov, 2006). Each bird species has a specific set of stereotypical movements that they use to hunt or eat.

The Kestrel gets 76 % of its prey hunting in the air. The decrease in hunting activity is observed after successful attacks, whereas after unsuccessful hunting the birds become more active.

Daily and circadian rhythms, hunting time and time of the victims' activity, food cache of the Common Kestrel, or Boreal Owl.

Predatory birds always should choose which prey to feed their chicks. This can affect the distribution of time and energy when hunting and raising chicks. It has been established that Kestrel will not be able to feed the brood only by insects, since they need to bring insects every 40 seconds, whereas rodents only need to be provided once every 75 minutes (Steen et al., 2012). Therefore, the composition of the food is also important, namely, the presence of proteins, the content of which in vertebrates is much higher.

The size of the hunting area also affects the composition of the diet. For example, the hunting territory of the Montagu's Harrier is larger than the hunting area of the Hen Harrier, *Circus cyaneus* (Linnaeus, 1766), partly because of more diversity is observed in the nutrition of the Montagu's Harrier (Garcia, Arroyo, 2005). The sedentary species are also characterized by a difference in the hunting area in the nesting and non-nesting periods. For example, a male barn owl occupies a much larger area in the non-nesting season than in the nesting period, due to the fact that it doesnt bother about the nest or covey during this period.

Victim's factors

Behavior. The composition of a predator's diet may depend on the behavior the species of the victim and their sex. Some birds, such as the Common Kestrel, can see the odorant rodents marks in the UV spectrum. It was found that the kestrels preferred the odor marks of male voles compared to females and immature individuals. However, studies of selectivity between Common Vole, *Microtus arvalis* (Pallas, 1779), and Bank Vole, *Myodes glareolus* (Schreber, 1780), by odor marks have not get positive results. This can also be due to the fact that males not only mark their routes, but also usually mark their territory, that`s why their marks are much better noticeable.

Weather. Despite the small size of the body, and therefore the imperfection of thermoregulation, rodents are able to tolerate a variety of temperature conditions due to various adaptations (seasonal change of fur, digging holes, in which the animal shelters not only from low, but also from high temperatures). Some rodents with the onset of the cold weather fall into hibernation (ground squirrels, birch mice). Rain or other precipitation also significantly reduces the activity of rodents, which affects their hunting efficiency. Lightening conditions also deteriorate during precipitation.

Polyphagia among birds of prey

Most Falconiformes and Strigiformes like other predators are characterized by polyphagia, or at least oligophagy. Only some species of birds of prey can be attributed to stenophages, among which the best example is the Snail Kite, *Rostrhamus sociabilis* (Vieillot, 1817), that eats almost exclusively mollusks of the genus *Ampullaria*. All other birds of prey may, under certain conditions, switch to other feeds.

Spatial change

Biotope variability

Meadow. Most representatives of birds of prey can hunt at the meadow (except the Tawny Owl and the Eurasian Pygmy Owl that are exclusively forest species, as well as the little owl, which rarely hunts at the extensive open areas), as it is an open biotope suitable for the large variety of potential victims. The prays are in the meadows all the time, and temporary stay is often associated with occasional occurrences or seasonality in the lives of animals. However, the territory is associated with the potential victims of falconiformes and strigiformes initially due to the availability of producers and consumables of the first order. Among our model species, all falconiformes hunt at the meadow, but the Common Kestrel and the Common Buzzard are most often choose the low-grass biotopes, while the Montagu's Harrier and the Lesser Spotted Eagle can also hunt in high grasses, reeds, or within the shrubs. The Long-Eared Owl and the Western Barn Owl as well as Buzzard and Kestrel, also prefer hunting in low-grass areas while flying at low altitude above the grass in search of prey. The Eurasian Eagle-Owl hunts all over the meadow. Due to the difference between the places for getting fodder, the way of searching for prey and the type and altitude of flight are different. The size of the victims and the range of food also differ.

The high grass on the moisture soils most often is inhabited by the following animals: the European Water Vole, *Arvicola amphibius* (Linnaeus, 1758), Voles (*Microtus*), less often the Muskrat, *Ondatra zibethicus* (Linnaeus, 1766), a significant number of terrestrial nesting birds (in particular: the Pipits *Anthus* sp. Bechstein, 1805, the Wagtail *Motacilla* sp. Linnaeus, 1758, the Warblers *Acrocephalus* sp. J. A. Naumann and J. F. Naumann, 1811 and the Grass Warblers, *Locustella* sp. Kaup, 1829, the Common Reed Bunting, *Emberiza schoeniclus* (Linnaeus, 1758), less often the Stonechats, *Saxicola* sp. Bechstein, 1802) and two species of lizards (the Viviparous Lizard, *Zootoca vivipara* (Lichtenstein, 1823), the Sand Lizard, *Lacerta agilis* Linnaeus, 1758) and the Grass Snake, *Natrix natrix* (Linnaeus, 1758) from reptiles.

The Harrier and the Spotted Eagle find their forage in the meadows using no fast, active straight flight or static soaring. During such a flight, the birds move at a moderate speed that enables them to maneuver and dramatically change their direction of movement towards the prey.

On the arid meadows, where grassy cover is dwarf and sometimes is degraded, the population consists of various species of voles, Mice, *Apodemus* sp. Kaup, 1829, terrestrial nesting bird passeriformes (in particular: Larks, *Alauda* sp. Linnaeus, 1758, pipits, wagtail, stonechats and reptiles — *Lacerta agilis* and *Natrix natrix*).

In such a biotope, the fodder is usually obtained by the Common Buzzard and the Common Kestrel. Buzzard, rarely Kestrel, seek out of prey using either active straight flight or static soaring. At the same time, both species, noticed the prey, use shaky flight, or hanging. If necessary, they can switch over the peak and attack a potential victim.

Marshes. The Montagu's Harrier and the Lesser Spotted Eagle much less often — the Common Buzzard can hunt at the marshes. And the Common Kestrel practically never hunts at the swampy territories. This is certainly related to the potential victim assortment that inhabits the biotope. Most model species of strigiformes avoid this biotope, but the

Eurasian Eagle-Owl feels great on the swamps. This is due to the fact that the marshes have a much smaller human disturbance factor and, most importantly, there is the largest species diversity of nutrition object. In addition, the Eurasian Eagle-Owl does not favor of one special type of feed, but eats almost all smaller animals, or which it can hunt. It should be noted that, all our model species of both falconiformes and strigiformes are often encountered in its diet.

The marsh by itself is covered with higher vegetation than on meadows. Therefore a humidy or wet biotope is inhabited mainly by amphibians, some medium-sized mammals and small Passeriformes, that are able to camouflage themselves well and hide their nests among plants. Therefore, the diet of Falconiformes that live at the marshes includes primarily amphibians, in particular frogs, and mammals — voles and muskrats. Medium-sized birds — waders and rails, became a prey to predators most often in ecotones or near human habitats, near they nest. And the victims of small passeriformes are mostly young birds (chicks) or birds that are temporarily in this habitat.

Arable land. All four model species of Falconiformes and four species of Strigiformes (the Long-Eared Owl, the Western Barn Owl, the Little Owl and the Eurasian Eagle-Owl) hunt over the arable land. However, due to biological features and some adaptations, the lesser spotted eagle, the Montagu's Harrier and the Eurasian Eagle-Owl search for prey in this biotope mainly during the autumn migrations and resettlement of young individuals (the Eurasian Eagle-Owl). This is probably related to their movement and seasonal movement of prey (changing the biotopes of the distribution of basic or available feed). The Falconiformes birds of prey are able to acquire birds and mammals at the arable land equally. The forage of predators is enriched here by representatives of Passeriformes, Charadriiformes, some Galliformes and Rallidae; temporarily Columbiformes and Cuculiformes, can happen in this biotope, and sometimes the representatives of the anatidae also occur in case of astatic reservoirs presence.

The open biotope territory allows predators to spot a potential victim from afar and therefore catch it by surprise, or use certain hunting techniques. The arable land makes for buzzard and kestrel possible to wait for the attack on the victim, which is a typical for their hunting. Birds hang in one place, tracking the movements and behavior of the victim, and then quickly attack by nosediving.

The other two model species — the Montagu's Harrier and the Lesser Spotted Eeagle, catch their prey on the rable land by moving from a soaring flight to nose-dip attack, or — from a equilibrium flight to a sharp attack, using the possibilities of sharp maneuver.

The owls hunt mainly on the periphery using the perch (transmission lines, trees, shrubs) from which the territory is well viewed. They can also slowly soar over the land from a one perch to another in search of prey.

Such a difference in the ways of hunting is explained by morphological features of the aircraft (the width and length of the wings, their posture, the size of the tail and the bird itself) in different species of birds of prey.

Shrubs. In fact, none of our model falcon species can hunt in shrubs. It was shown by observations that only the Montagu's Harrier can hunt over rarefied shrubs in ecotones, on the edge of forests with swamps, meadows, or less often — arable land.

However, Strigiformes feel great in this biotope, especially in rarefied shrubs where they are almost always hunt from the perch. This is due to the fact that, unlike the Falconiformes, they rely much more on hearing than on vision while they hunt. It should also be noted that many species of Passeriformes, which hunted by owls, gather in shrubs for night lodging.

In this biotope, birds most often catch victims (small or young birds) frightened by the shadow or presence of the predator itself, or predators get "the reward" of weakened

or injured animals. The model species hunting in the shrub biotope in other cases is not effective at all.

Forests/Deforestation territory. Hunting in the place of deforestation is similar to hunting in arable habitat. However, not all of our model species use such territories for forage searching that is primarily related to the habitats of the birds themselves and their behavior peculiarity. For example, the Montagu's Harrier and the Common Kestrel prefer to feed (and nesting) on the open areas. Although deforestation territory, as a part of forest management, is often not open land surrounded by trees. Therefore, these two species, mentioned before, visit deforestation territory in search of forage only when it is located on the outskirts of the forest. In other cases, they are there during the migration period.

Two other species — the Common Buzzard and the Lesser Spotted Eagle, hunt on the deforestation territory, but most often on the large ones. These birds are more likely to rest within the small cutting areas, but, sometimes, they make hunting flight because of their behavior peculiarity. However, the species diversity of the victims and their availability in this biotope do not provide such hunting effectiveness as in the biotopes of meadows, arable land, or marshes.

Sometimes it is possible to observe the hunting of the Common Buzzard in a continuous forest with sparse stands. Such behavior is typical for the Common Buzzard in the spring when there are no leaves on the trees. We have repeatedly observed such hunting in forest parks, rarely in forest properties in Lviv.

The Tawny Owl and the Eurasian Pygmy Owl, which are typical forest species, hunt in this biotope. Pygmy Owls hunt in different successional stages and along inner forest edges, which offer elevated perches and a greater availability and accessibility of prey (Strøm, Sonerud, 2001; Braunisch et al., 2018, 2019). Unlike the Eurasian Pygmy Owl, the Tawny Owl prefers deciduous forests, mainly hunts in the thick of the forest and doesn't anchor to the lawns. Sometimes the Eurasian Eagle-Owl can hunt in the forest, but this happens in sparse forests due to the large size of the bird. Therefore, it mainly hunts a variety of birds or mammals at the edges of forest.

Zonal changes

Using falconiformes as an example, we pointed to the low efficiency of the hunting process in the cuttings biotope of small non-wooded areas. However, everything looks different in the zonal section. Birds inhabiting the central and northern parts of the forest area with few open landscapes adapted to forage searching in a restricted area. The long-migrated birds can also hunt in the areas that are virtually unused on their nesting territory, or do not visit in other times of the year (such as mountain slopes and valleys, woodlands, semi-deserts, etc.).

For example, the Gyrfalcon, *Falco rusticolus* Linnaeus, 1758, mainly hunts for seabirds on the seashore of the north, and in taiga — on Galliformes. The representatives of the *Aquila* genus often hunt marmots and ground squirrels during migrating in the mountainous or steppe areas, but in meadows and river valleys of the temperate zone rats, foxes, small birds and amphibians serve as food.

Changes in time

Behavioral and nutritional changes in kestrels and, less often, in other model species occur not only in space, but also in time. This is a regularity of adaptations to survival under variable climatic factors and environmental conditions. In addition, the diet of birds can change with age. Older birds are more experienced in finding and capturing prey, and young birds are more often satisfied with the widespread and accessible species of prey.

Daily changes. Based on visual observations in Kharkiv, it is established that kestrels are active mainly in the morning (9:00–12:00) and in the evening (16:00–19:00), and at this period they hunt predominantly sparrows, rarely murine rodents (Viter, 2011). Interestingly, they are often hunted at twilight and even in the dark.

Our observations, conducted in Lviv, confirm that Kestrels start to hunt in the morning. Birds on the outskirts of the city's residential neighborhoods fly to feed from 7:30 to 8:00 in the morning. The hunting of the Kestrels finishes about 19 pm, rarely later, but not after 20:30. Similar daily rhythms are observed in many birds of prey (especially small and medium size birds), which is primarily related to the biological rhythms of their prey.

We see the opposite behavior in owls, as they are mostly active at night. However, to consider owls exclusively as night predators is a mistake, since there are some daytime species, such as the Northern Hawk-Owl. There is also such a misconception that the Eurasian Pygmy Owl is a night predator. In fact, he hunts at dusk or daytime. The peak of activity of the most owls begins about half an hour before sunset and lasts 2–3 hours after sunset. Then there is a significant decrease in activity, after which the activity increases again 2–3 hours before dawn and lasts for about 0.5–1 hours after sunrise (depending on the species and time of year).

Seasonal changes. Seasonal changes in the nutrition of birds of prey are closely related to potential victims and seasonal manifestations of their biological characteristics. So, the Common Buzzard are the first, who return from wintering places. The main food for them at this time are mice (*Mus* sp.). However, in the midst of the nesting season, the feeding ration of buzzards changes: voles (*Microtus* sp.) beginning to prevail in diet, also lizards, small birds and frogs appear in the diet composition. There are also changes in diet composition of the Common Kestrel due to changes in the activity of victims (small Muriformes and Soriciformes) and the activity and flight of large-sized insects.

Owls have the same seasonal changes in diet as daytime birds of prey. The diversity depends on the size of the owl and can vary greatly in different years, depending on the predominance of a particular type of prey. For example, in Lviv, the diet of the tawny owl is mainly consist of representatives of the Muridae family. However, the Tawny Owl begins to hunt almost exclusively for the Common Frog, *Rana temporaria* Linnaeus, 1758, in the spring during the breeding season of this species.

Annual changes. Annual changes in nutrition of Falconiformes and Strigiformes depend on the breeding cycles of potential victims. In particular, this is due to the years called "mousy", the population waves of animals, and the climat conditions of a particular year. It is shown in literature sources that predators are able to "switch" to those types of feed that reach the maximum values of their numbers in a particular year, and therefore become more accessible or easier for hunting.

Thus, the frequency of eating bugs increases in the years of their large number population, and the diet of birds changes accordingly. Years of massive reproduction of mice or voles also lead to minimalization of species selectivity of birds of prey.

Thus, the frequency of eating bugs increases in the years of their large number population (e. g. fluctuations in the quantity of the Common Cockchafer, *Melolontha melolontha* (Linnaeus, 1758), in different years), and the diet of birds changes accordingly. In such years, the cockchafers often occur in the diet of birds of prey, even in large owls, which rarely eat insects (Western Barn Owl, Long-Eared Owl etc.). Years of massive reproduction of mice or voles also lead to minimalization of species selectivity of birds of prey, that hunt mainly for mass types of victims.

Conclusions

Almost whole activity Falconiformes and owls, with the exception of the breeding season, directed to finding food. We can conclude from this statement that the nutrition

has exceptional value for birds. The role of the trophic factor in the life of birds of prey can be estimated by its influence on the population, in particular fertility, mortality, immigration and emigration. The size and energy value of eggs are positively correlated with metabolism activity of the female bird during egg formation and the probability of hatching of all chicks in the nest increases. The sex ratio of birds of prey depends on the availability of feed and the number of males among chicks exceeded the number of females in hungry years. Regarding mortality, the direct lethal impact of the trophic factor on birds of prey is a rare fact, since they can live without food for a long time. However, prolonged adverse weather conditions can complicate or even make hunting impossible, leading to the exhaustion and even death of birds, which is often observed in winter. All types of movement of birds of prey in space are associated with seasonal variations in food availability and directed at balancing predator numbers in regard to the number of victims and finding new nesting areas. This proves that the availability of feed plays a major role in the predator's immigration or emigration.

The whole chain of events is required in order to catch one single nutrition object by predator. Only one of the eight possible outcomes of the meeting will lead to the death of the prey. In general, the predator-victim interaction is a complex dynamic system that depends on the properties of the organisms that interact with each other and the factors of environment, where this interaction takes place. Thus, the factors affecting the victim should be separated — "prey factors" and predator factors — "predator factors". Moreover, different factors affect the different stages of their interaction.

References

Arroyo, B. E. 2006. Diet composition influences annual breeding success of Montagu's Harriers *Circus pygargus* feeding on diverse prey: Capsule Diet diversity was positively related to nest failure in Montagu's Harriers. *Bird Study*, **53** (1), 73–78.

Aschwanden, J., Birrer, S., Jenni, L. 2005. Are ecological compensation areas attractive hunting sites for Common Kestrels (*Falco tinnunculus*) and long-eared owls (*Asio otus*)? *Journal of Ornithology*, **146**, 279–286.

Atamas, N. 2004. Some peculiarities of using the droppings of birds of prey for study of small mammals fauna. *Visnyk of L'viv Univ. Biology series*, **38**, 133–136 [In Ukrainian].

Bernard, N., Michelat, D., Raoul, F., Quéré, J. P., Delattre, P., Giraudoux, P. 2010. Dietary response of Barn Owls (*Tyto alba*) to large variations in populations of Common Voles (*Microtus arvalis*) and European Water Voles (*Arvicola terrestris*). *Canadian Journal of Zoology*, **88** (4), 416–426.

Birrer, S. 2009. Synthesis of 312 studies on the diet of the Long-Eared Owl *Asio otus*. *Ardea*, **97** (4), 615–624.

Braunisch, V., Roder, S., Coppes, J., Bollmann, K. 2018. Structural complexity in managed and strictly protected mountain forests: effects on the habitat suitability for indicator bird species. *5th European Congress of Conservation Biology (12th–15th of June 2018, Jyväskylä, Finland).*

Braunisch, V., Roder, S., Coppes, J., Froidevaux, J., Arlettaz, R., Bollmann, K. 2019. Structural complexity in managed and strictly protected mountain forests: Effects on the habitat suitability for indicator bird species. *Forest Ecology and Management*, **448**, 139–149.

Butet, A., Leroux, A. 2001. Effects of agriculture development on vole dynamics and conservation of Montagu's Harrier in Western French wetlands. *Biological Conservation*, **100**, 289–295.

Butet, A., Michel, N., Rantier, Y. et al. 2010. Responses of Common Buzzard (*Buteo buteo*) and Eurasian Kestrel (*Falco tinnunculus*) to land use changes in agricultural landscapes of Western France. *Agriculture, Ecosystems and Environment*, **138**, 152–159.

Castillo-Góómez, C., Moreno-Rueda, G. A 2011. Record of a Common Buzzard (*Buteo buteo*) nesting in an Abandoned Building. *The Journal of Raptor Research*, **45** (3), 275–277.

Dawkins, R. 2010. *The Extended Phenotype: The Long Reach of the Gene*. Astrel, Moscow, 1–512 [In Russian].

Elkins, N. 2004. *Weather and bird behaviour*. 3rd ed. Poyser, London, 1–280.

Galushin, V. M. 2005. *Adaptive strategies of birds of prey*. Abstracts of Thesis, Moscow, 1–49 [In Russian].

Garcia, J. T., Arroyo, B. E. 2005. Food-niche differentiation in sympatric Hen *Circus cyaneus* and Montagu's Harriers *Circus pygargus*. *Ibis*, **147**, 144–154.

Gavrilyuk, M. N. 2009. *Guidelines to the programme of the monitoring of birds of prey in Ukraine*. Cherkasy, 1–20 [In Ukrainian].

Honkavaara, J., Koivula, M., Korpimäki, E. 2002. Ultraviolet vision and foraging in terrestrial vertebrates. *Oikos*, **98**, 505–511.

Jenkins, A. R. 2000. Hunting mode and success of African Peregrines *Falco peregrinus minor*: does nesting habitat quality affect foraging efficiency? *Ibis*, **142**, 235–246.
Karyakin, I. V. 2004. *Feathered predators (Guidelines for the study of Falconiformes and Owls)*. Povolzhya, Nizhny Novgorod, 1–351 [In Russian].
Karyakin, I., Vasenkov, D., Dubynin, A. 2000. The Ural Owl in the Novosibirsk region — from the Red Book to freedom?. *Siberian Ecological Vestnik*, **13–14**, 58–61 [In Russian].
Kokko, H., Ruxton, G. D. 2000. Breeding suppression and predator–prey dynamics. *Ecology*, **81** (1), 252–260.
Koks, B. J., Trierweiler, C., Visser, E. G. 2007. Do voles make agricultural habitat attractive to Montagu's Harrier *Circus pygargus*? *Ibis*, **149**, 575–586.
König, C., Weick, F. 2008. *Owls of the world*. Christopher Helm, London, 1–529.
Korpimäki, E., May, C. A., Parkin, D. T., Wetton, J. H., Wiehn, J. 2000. Environmental- and parental condition-related variation in sex ratio of kestrel broods. *Journal of Avian Biology*, **31** (2), 128–134.
Krüger, O. 2004. The importance of competition, food, habitat, weather and phenotype for the reproduction of Buzzard *Buteo buteo*. *Bird Study*, **51**, 125–132.
Lõhums, A. 2011. Three-year periodicity in historical raptor-pesercution data: an indication of vole cycles? *Estonian Journal of Ecology*, **60** (2), 155–164.
Meyburg, B.-U., Graszynski, K., Langgemach, T. et al. *2008.* Cainism, nestling management in Germany in 2004–2007 and satellite tracking of juveniles in the Lesser Spotted Eagle (*Aquila pomarina*). *Slovak Raptor Journal*, **2**, 53–72.
Mykytyuk, O. 2000. *National Action Plans for the Conservation of Globally Vulnerable Bird Species*. SoftArt, Kyiv, 1–205 [In Ukrainian].
Nankinov, D. N. 2002. Present situation of population of owls in Bulgaria. *Berkut*, **11**(1), 48–60 [In Russian].
Newton, I. 2008. *The Migration Ecology of Birds*. Academic Press, London, 1–976.
Novikov, G. A. 2001. Some approaches and techniques for investigation of food and trophic relationships in mammals and birds. *The Russian Journal of Ornithology*, **10** (154), 673–687 [In Russian].
Paspali, G., Oruci, S., Koni, M., Wilson, I. F., Krystufek, B., Bego, F. 2013. Seasonal variation of small mammals in the diet of the Barn Owl (*Tyto alba*) in the Drinos River valley, southern Albania. *Turkish Journal of Zoology*, **37** (1), 97–105.
Reif, V., Tornberg, R., Huhtala, K. 2004. Juvenile grouse in the diet of some raptors. *Journal of Raptors Research*, **38** (3), 243–249.
Rejt, Ł. 2006. Does larder-hoarding affect the condition of chicks in urban kestrels? *Biologia, Bratislava*, **61** (2), 221–224.
Sergio F., Newton I., Marchesi L. 2005. Top predators and biodiversity. *Nature*, 436, 192.
Steen, R., Sonerud, G. A., Slagsvold, T. 2012. Parents adjust feeding effort in relation to nestling age in the Eurasian Kestrel (*Falco tinnunculus*). *Journal of Ornithology*, **153**, 1087–1099.
Strøm, H., Sonerud, G. 2001. Home range and habitat selection in the Pygmy Owl *Glaucidium passerinum*. *Ornis Fennica*, **78**, 145–158.
Terraube, J., Arroyo, B. 2011. Factors influencing diet variation in a generalist predator across its range distribution. *Biodiversity and Conservation*, **20** (10), 2111–2131.
Terraube, J., Arroyo, B., Madders, M., Mougeot, F. 2010. Diet specialisation and foraging efficiency under fluctuating vole abundance: a comparison between generalist and specialist avian predators. *Oikos*, **120** (2), 234–244.
Tsaryk Y. V. 2005. *Population ecology. Management of population*. Publishing house of LNU, Lviv, 1–100 [In Ukrainian].
Väli, Ü. 2004. Sex ratio of Lesser Spotted Eagle *Aquila pomarina* nestlings in good and poor breeding years: Capsule the ratio was female-biased in good years and male-biased in poor years, but did not differ from parity in the long term. *Bird study*, **51** (2), 189–191.
Väli, Ü. 2012. Factors Limiting Reproductive Performance and Nestling Sex Ratio in the Lesser Spotted Eagle *Aquila pomarina* at the Northern Limit of Its Range: the impact of Weather and Prey Abundance. *Acta Ornithologica*, **47** (2), 157–168.
Valkama, J., Korpimäki, E., Wiehn, J., Pakkanen T. 2002. Inter-clutch egg size variation in Kestrels *Falco tinnunculus*: seasonal decline under fluctuating food conditions. *Journal of Avian Biology*, **33**, 426–432.
Verdal, T., Selås, V. 2010. A comparison of Goshawk summer diet in three areas with different breeding density in western Norway. *Ornis Norvegica*, **33**, 110–117.
Viter, S. G. 2011. The raptors (Falconiformes) of Kharkov city: features of ecology and interspecific relations. *Proceedings of the Zoological institute of the RAS*, **315** (1), 89–97 [In Russian].
Yablokov, A. V. Yusufov, A. H. 2006. The doctrine of microevolution. *In*: *Evolutionary doctrine*. Vysshaya Shkola, Moscow, 93–202 [In Russian].
Yatsjuk, Ye. A. 2008. Small mammal's fauna of elevated oak forest of National park "Gomilshanski lissy" according to data on Tawny owl pellets analyzing. *The Journal of V. N. Karazin Kharkiv National University. Series "Biology"*, **814** (7), 132–139 [In Ukrainian].
Żmihorski, M. 2007. Weather-dependent variation in the cold-season diet of urban Kestrels *Falco tinnunculus*. *Acta Ornithologica*, **42** (1), 107–113.

Zuberogoitia, I., Martínez, J. E., Martínez, J. A. et al. 2006. Influence of management practices on nest site habitat selection, breeding and diet of the Common Buzzard *Buteo buteo* in two different areas of Spain. *Ardeola*, **53** (1), 83–98.

Received 30 April 2020
Accepted 26 October 2020