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L. Kharchenko
Poltava V. G. Korolenko National Pedagogical University
2, Ostrohradskyi street, Poltava, 36003, Ukraine
harchenko.lp1402@gmail.com
ORCID: 0009-0000-6208-464X
I. Lykova
H. S. Skovoroda Kharkiv National Pedagogical University
29, Alchevskyh street, Kharkiv, 61002, Ukraine
irlyk16@gmail.com
ORCID: 0000-0003-1347-2077
A. Koval
Poltava Institute of Economics and Low, Open University
of Human Development Ukraine
6, Monastyrska street, Poltava, 36000, Ukraine
*indivwork@gmail.com*ORCID: 0000-0002-8572-7000
K. Ponomarova
H. S. Skovoroda Kharkiv National Pedagogical University
29, Alchevskyh street, Kharkiv, 61002, Ukraine
kate67261@gmail.com
ORCID: 0009-0003-1709-4920

CHARACTERISTICS OF BIRD EGGSHELL COLORATION DEPENDING ON NEST LOCATION

Based on the analysis of egg collections of different ecological groups of birds and various literature sources, a summary of scientific studies on morphological adaptations related to the color of eggshells in birds is given. Eggshell color in birds is a morphological adaptation with a masking function that depends on nesting conditions. The article examines egg collections of birds with an open nesting type: Eurasian skylark (ground-nesting), Eurasian chaffinch (crown-nesting), and Red-backed shrike (bush-nesting). The study confirmed the high variability of eggshell color in birds with an open nesting type, which allows clutches to be invisible which contributes to successful nesting. The correlation between the location of the nest and the color of the eggshells of the studied bird species was analyzed, and the peculiarities of this correlation were determined.

Keywords: *coloration of bird eggshells, types of nesting, morphological adaptations, egg collections.*

Introduction. One of the important areas of ecology and evolutionary theory is the study of the diversity and mechanisms of adaptation to biotic and abiotic factors of the environment. Biochemical, physiological, behavioral, and morphological adaptations in birds have been formed depending on environmental characteristics. The color of eggshells is one of the morphological adaptations that serve one of the main functions – camouflage, being an adaptation to the ecological conditions of nesting (location of the nest). This feature is the most pronounced in birds with an open-nest type of nesting. A high metabolic rate, homothermy, multiple trophic relationships, and the ability to fly actively have allowed birds to occupy a variety of ecological niches. It is well known that birds can be divided into open, semi-open, and closed nesters based on their nesting habits. The greatest variability in eggshell pigmentation is found in open-nesting birds because the masked color of the eggshell allows the clutches to be invisible to predators.

It has been found that the color of bird eggshells is determined by two pigments: biliverdin (green color) and protoporphyrin (reddish-brown color). Varying concentrations of these pig-

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ments, along with the white calcium carbonate that underlies the shell, give the shell a color that ranges from dark blue to greenish-white and rich brown. Studies have shown that dark eggs tend to be more common in regions with lower solar radiation intensity. This trend persists even when the nests are of different types. The researchers concluded that the eggshell brightness and color should be associated with the ambient temperature. Darker eggs absorb more heat, which is an advantage in cold regions because the embryo inside the egg can develop at a certain temperature. Of particular note is the eggshell of *Cuculus canorus* Linnaeus 1758, which has a different structure that is an evolutionary adaptation to prevent egg cracking.

A. Gosler, J. P. Higham, and S. J. Reynolds (Gosler, Higham & Reynolds, 2005) hypothesized that protoporphyrin pigments may compensate for reduced eggshell thickness caused in part by calcium deficiency. The article by J. M. Aviles and co-authors (Aviles, Soler & Perez-Contreras, 2006) states that the ultraviolet reflection from eggshells is important for recognizing eggs by closed-nesting birds. J. J. Sanz and V. García-Navas (Sanz & García-Navas, 2009) examined the influence of pigment spot distribution, size, and intensity on eggshell physical characteristics and reproductive parameters related to nesting conditions. Z. A. Aidala and M. Huber (Aidala & Hauber, 2010) analyzed the peculiarities of birds' vision (tetrachromatic) that allow them to distinguish their eggs from those of the nest parasitic birds. The article by Cassey et al. (2012) quantifies the two most important egg pigments, i.e., biliverdin and protoporphyrin, and tests how these pigments affect the physical parameters of eggshell coloration, and whether this affects phylogenetic species affiliation and pigment diversity.

Research by D. Lahti and D. Ardia (Lahti & Ardia, 2016) examines egg pigmentation, which affects the coefficient of light transmission through the shell and the degree to which it heats up by absorbing solar radiation. D. E. Duursma and co-authors (Duursma, Gallagher, Price & Griffith, 2018) conducted the first continental study (Australia) of the functional characteristics of birds, revealing a regularity between nest type, egg length, and climatic conditions of the region. Poláček, Bartíková, & Hoi (2017) studied eggshell pigmentation in sparrows and experimentally confirmed that egg pigmentation is also closely related to the order in which females lay their eggs. The first and last eggs were less pigmented, and females placed darker-pigmented eggs in the central part of the nest.

P. Cassey and colleagues (Cassey et al., 2012) quantified the concentrations of two major avian eggshell pigments (protoporphyrin and biliverdin) from different eggshell samples deposited at the Natural History Museum (Tring, UK). The researchers examined how the two pigments are related to eggshell coloration, and whether pigment concentration and eggshell color diversity correlate with phylogenetic relationships among species; they tested several comparative hypotheses regarding the relationship between concentrations of the two pigments and evolutionary traits and nesting ecology. Protoporphyrin concentration was found to be associated with a higher probability of nesting in a tree hole and on the ground, while biliverdin concentration was associated with a higher probability of open nesting (Cassey et al., 2012) when birds lay bright-color eggs in conspicuous locations. D. Henley (Henley, 2012) hypothesized in his dissertation research that since an egg with a bright shell is exposed to a greater risk of predation, the female incubates the clutch very tightly, and the male also takes an active part in this process (incubating alternately with the female or bringing her food so that she can stay on the nest).

The eggshells of open-nesting birds are more intensely pigmented than those of species that nest in burrows or tree holes. The main function of the pigment in this case is to camouflage the eggs. Eggshell pigmentation is also important for the thermoregulation of the internal contents of the egg, acting as a buffer between the embryo and the environment. The eggshell controls the amount of light that enters the egg, where the embryo develops.

Sunlight also reveals another interesting function of eggshell pigmentation, namely, photodynamic antimicrobial properties. Protoporphyrin, when heated in the sun, can virtually destroy gram-positive bacteria (e.g., staphylococcus) from outside the egg, acting as an external immune system for the developing embryo (Cassey et al., 2012). In the course of oological research, the reasons that determine the color of eggshells in different ecological groups of birds were found,

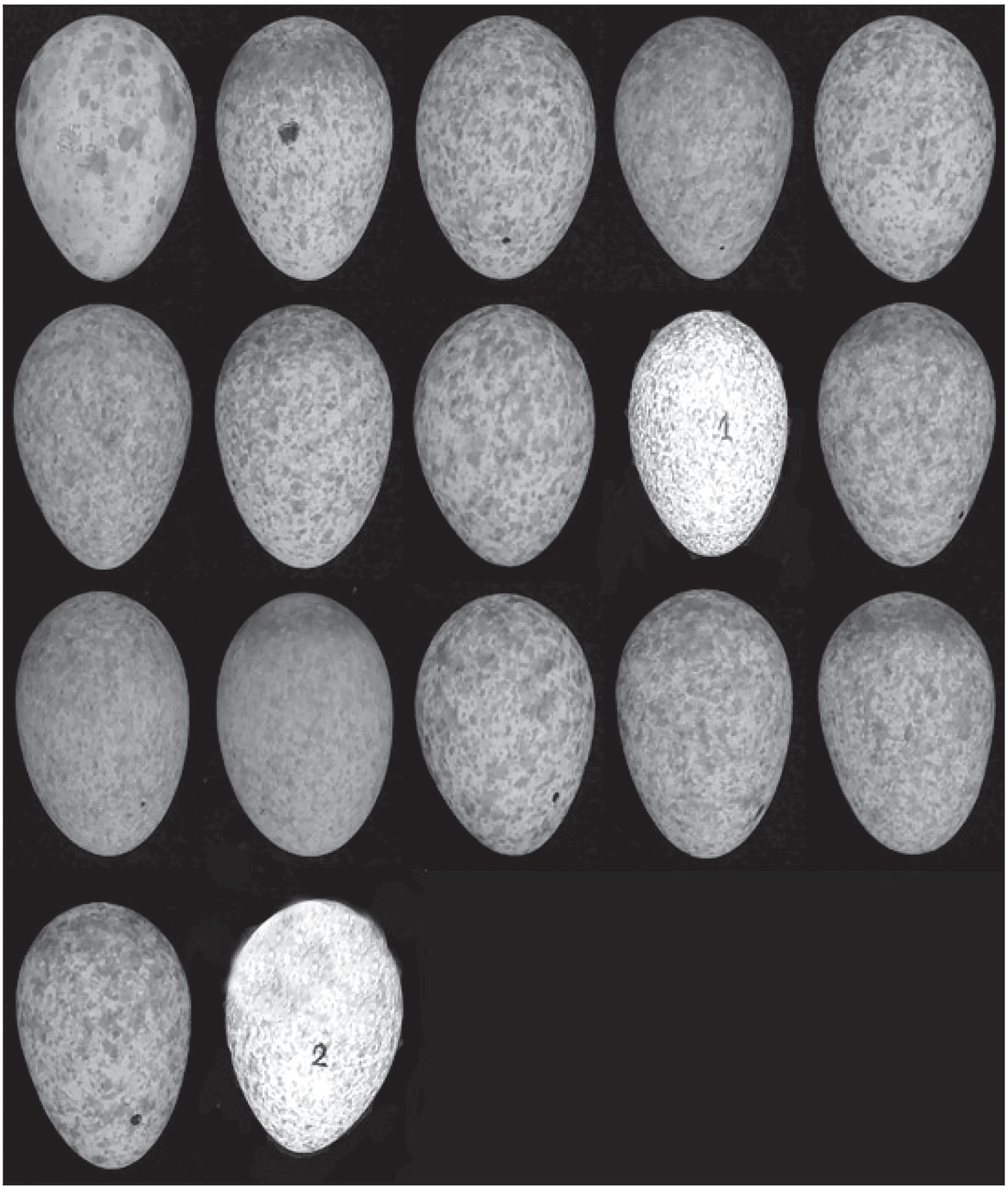

Figure 1. **A collection of eggs of *Alauda arvensis* Linnaeus, 1758**

namely: temperature; camouflage from predators; mitigation of the harmful effects of ultraviolet light on the DNA of the embryo; identification of the eggs of brood parasites; different antimicrobial properties of the eggshells of different colors.

After analyzing the various literature on the pigmentation of bird eggshells, we set the goal of the study: to identify the peculiarities of eggshell coloration in relation to nest location.

Materials and methods. The following collected oological material was used in the preparation of this article: a collection of eggs of *Alauda arvensis* Linnaeus, 1758 (Fig. 1), a collection of eggs of *Lanius collurio* Linnaeus 1758 (Fig. 2), and a collection of eggs of *Fringilla coelebs* Linaens, 1758 (Fig. 3). The research was conducted using the Kostin method (Kostin, 1977). Its essence is that the external structure of the egg is determined by a set of the following features: shape, color, and pattern location. The size and dimensions of eggs were determined by two parameters: length and diameter, which distinguish the following basic shapes of bird eggs: round or spherical; elongated or oval; elliptical and regular ovate.

The eggshell color consists of two main elements –– the background and the pattern. According to the density of the eggshell pattern, the following types are distinguished: simple coloring without pattern; very sparse pattern; sparse pattern; dense and very dense pattern. The localization of the eggshell pattern was determined visually. According to the localization of the pattern, we distinguished: a pattern shifted to the blunt (infundibular) end (inf); a pattern shifted to the sharp (cloa-

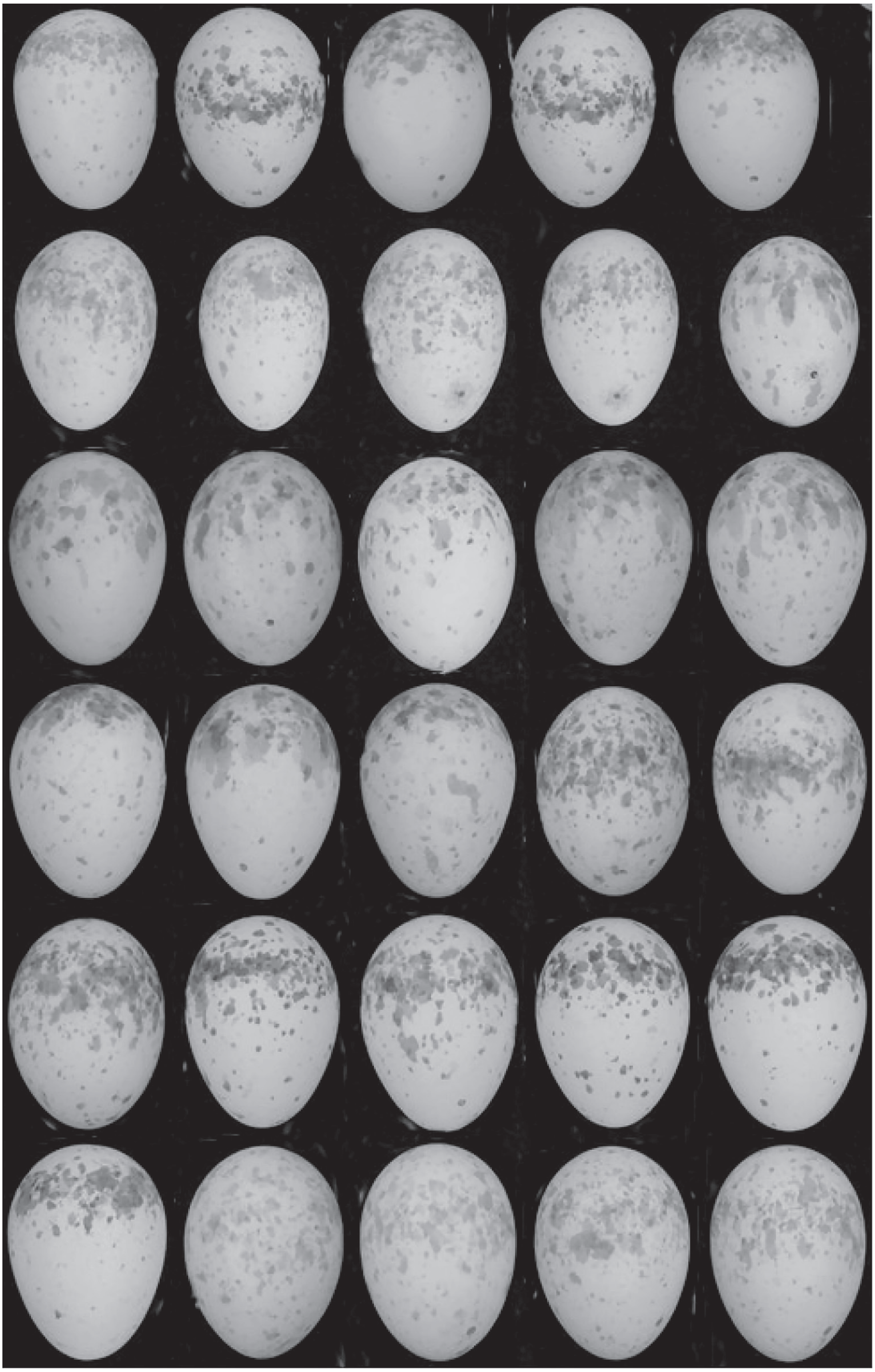

Figure 2. **A collection of eggs of *Lanius collurio* Linnaeus 1758**

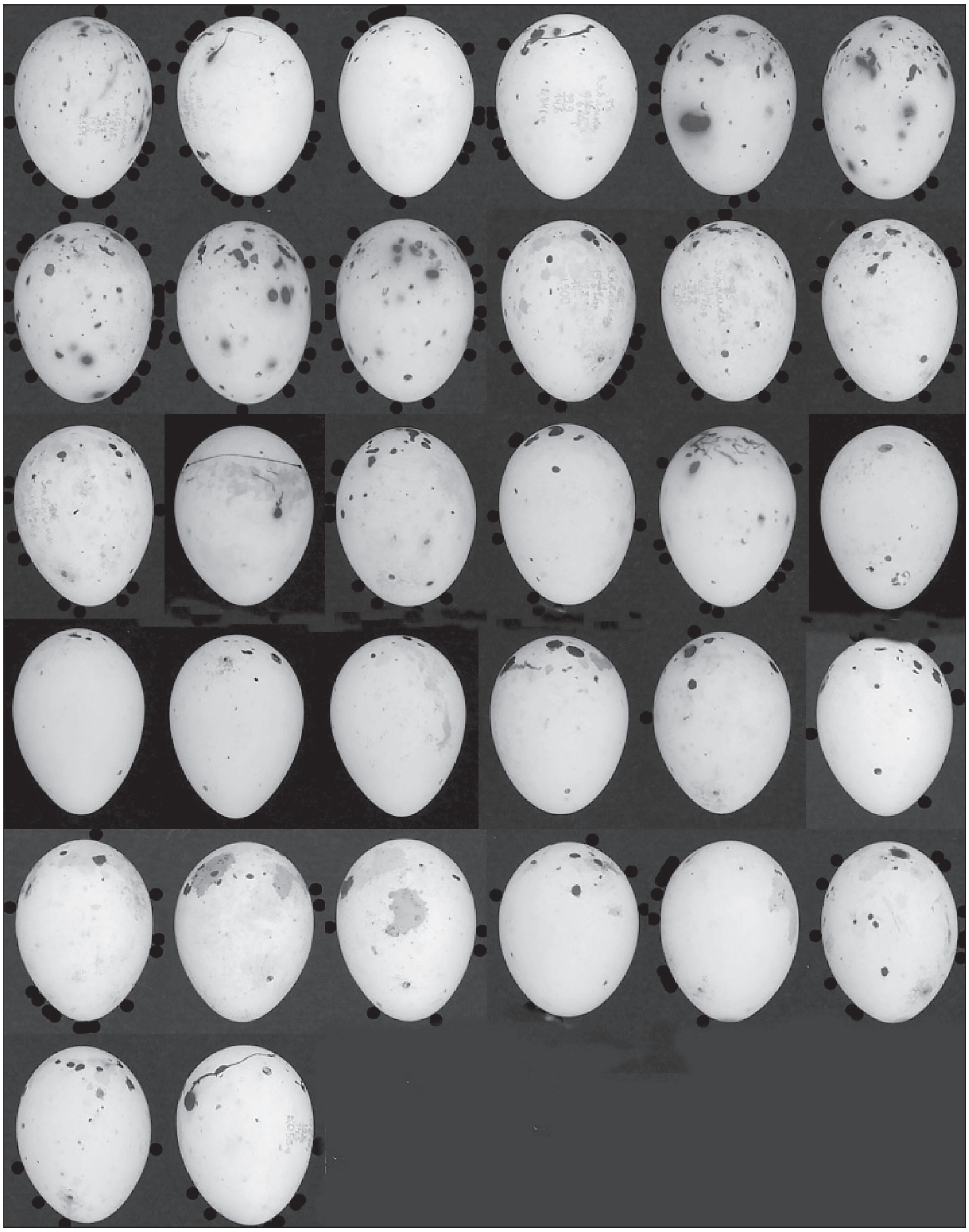

Figure 3. **A collection of eggs of *Fringilla coelebs* Linaens, 1758**

cal) end (clo); a pattern placed evenly (even); pattern elements placed on both the blunt and sharp ends (info/clo); a pattern forms a belt in the equatorial zone (equat) (Mytiai, 2008).

Results. For protection and camouflage of their eggs, birds build their nests on the ground in grassy thickets, in dense bushes, and between dense branches of trees. The variability of nest locations determines the diversity of eggshell colors and allows for studying the patterns of evolutionary changes in egg color under different environmental factors. By studying the color and location of eggs, it is possible to monitor the status of bird populations and their ecological variability and to establish phylogenetic relationships between different bird species.

Alauda arvensis is characterized by nesting on the ground among low but thick grass, in a pit between young tree sprouts. Nests are sometimes found at the base of tree trunks or even in the open place. The color of the eggshell changes depending on the nest location, which is visible in the collection (Fig. 1). The nest is made of dry grass stalks, roots, and straw. The inner part of the nest is lined with finer, softer blades of grass interwoven with horsehair.

Analysis of the collection material showed that the background of *Alauda arvensis* eggshells is beige, brown, and, in some cases, blue-gray. On the whole surface of the eggshell, dark gray-brown spots of various sizes are densely arranged, sometimes a so-called «corolla» is formed at the blunt end of the egg. The eggshells of birds whose nests are on the ground among the sparse grass have a much lower pattern density and a lighter background color. Of 19 *Alauda arvensis* eggs examined, twelve had a brown eggshell background and seven had a beige-grayish color.

Lanius collurio is a typical bush bird. The nest is built among the dry stalks of herbaceous plants, in bushes, sometimes low on a tree. The nests are quite large, cup-shaped, with strong thick walls made of thick dry stems, narrow stems of herbaceous plants (mainly cereals), roots, and rhizomes of herbs. The lining of the nest consists of dry grass stalks, panicles of grasses, wool, and feathers woven into the walls of the nest.

The eggshells of these birds have a beige, yellowish, or light green background with a slight blue tinge. On these shell backgrounds, are gray-purple, brown, and dark brown spots, localized mainly in the "corolla" at the blunt end or along the egg's equator. In some cases, the spotting occurs over the entire egg surface.

All 26 *Lanius collurio* eggs from the examined collection had a yellowish background and a spotted pattern localized (1) in the "corolla" at the blunt end in 17 eggs, (2) at the equator in eight eggs, (3) uniformly in one egg. Pattern density was insignificant on all eggs. Despite the sparse pattern of *Lanius collurio* eggs, the spotting is higher than in tree-nesting birds, which allows the eggs to be successfully camouflaged in scrub.

Fringilla coelebs lives in forests of different types, parks, and near human settlements. It builds nests in trees near the trunk or in a fork of dense branches. The nest of *Fringilla coelebs* is cup-shaped; to hide the nest, the birds weave lichens, mosses, and pieces of bark collected nearby into the outer wall, so the nest is almost invisible against the tree bark background.

The eggshell of *Fringilla coelebs* has a blue background with some greenish tinge and linear-spotted or spotted patterns located on the blunt end of the egg, sometimes on the blunt and pointed ends. The image is sparse, the main masking function belongs to the background. The eggshell coloration helps this bird to be completely invisible among the branches and green leaves. Depending on the tree on which the nest is located, the oological indicators of the eggs may vary.

All 32 *Fringilla coelebs* eggs in the collection had a blue background of the eggshells; 27 eggs had a spotted pattern and five eggs had a linear-spotted one. The pattern was localized on the blunt egg end, only in one egg it was present on both ends. The pattern in all examined eggs was classified as sparse.

Conclusions. Intra clutch and intraspecies variability of the color of bird eggshells is manifested in the intensity of pigmentation of the background and pattern, in the shape of pattern elements, and the character of their location on the eggshell surface. Color variability of the eggshells of birds from the studied collections corresponds to the phenomenon of intrapopulation polymorphism. Thus, according to the background color of the eggshell, we distinguished three morphs (brown, sandy, and gray) in *Alauda arvensis*, three morphs (beige, sandy, and greenish-blue) in *Lanius collurio*, and two morphs (blue and green) in *Fringilla coelebs.* Each ecological group of birds is characterized by a certain type of eggshell background color, which provides the best result in protection against predators. The above-mentioned types of shell coloration in the egg collections studied can also be considered an effective way of masking clutches in birds with an open nesting type.

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ОСОБЛИВОСТІ ЗАБАРВЛЕННЯ ШКАРАЛУПИ ЯЄЦЬ ПТАХІВ ЗАЛЕЖНО ВІД МІСЦЯ РОЗТАШУВАННЯ ГНІЗДА

Л. П. Харченко І. О. Ликова, А. А. Коваль, К. О. Пономарьова

Полтавський національний педагогічний університет імені В. Г. Короленка

Харківський національний педагогічний університет імені Г. С. Сковороди

Полтавський інститут економіки і права ЗВО «Відкритий міжнародний університет розвитку людини «Україна»»

У статті за результатами аналізу колекцій яєць різних екологічних груп птахів та різних літературних джерел узагальнено наукові дослідження щодо морфологічних адаптацій, які відносяться до забарвлення шкаралупи яєць у птахів. Зазначено, що морфологічна адаптація – забарвлення шкаралупи яєць у птахів – одна із функцій маскування та пристосування до умов гніздування. У статті досліджувалися колекції яєць птахів з відкритим типом гніздування: жаворонок польовий (наземногніздний), зяблик (кроногніздний) та сорокопуд терновий (кущогніздний). Дослідження підтвердило положення про високу варіабельність забарвлення шкаралупи яєць птахів з відкритим типом гніздування, що дозволяє кладкам бути непомітними і сприяє успішному гніздуванню. Проаналізовані місця розташування гнізд досліджених птахів із забарвленням шкаралупи яєць птахів різних екологічних груп. Установлені особливості такої залежності між цими показниками.

Ключові слова: *забарвлення шкаралупи яєць птахів, типи гніздування, морфологічні адаптації, колекції яєць.*

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