- 8. Briskin D.P. Medicinal plans and phytomedicines. Linking plant biochemistry and physiology to human health / Plant Physiol, 2000; №124: P.507–514.
- 9. Hatfield R., Vermerris W. Lignin formation in plant. The dilemma of linkage specificity /Plant Physiol. 2001. 126. P. 1350–1357.
- 10. Henerozova I.P., Maevskaya S.N., Shuhaev A.G Inhibition of metabolic activity mytohondryy etyolyrovanyh peas seedlings enhancing by water stress. / Physiology of Plants, 2009; 56(1): 45–52.
- 11. Lee B.R., Lee B.R., Kim K.Y., Jung W.J Peroxidases and lignification in relation to the intensity of water-deficit stress in white clover (Trifolium repens L.)/Journ. of Exp. Botany. 2007. 58. № 6. P. 1271–1279.

 12. Crozier A., Burns J., Aziz A.A. Antioxidant avonols from fruits, vege-
- 12. Crozier A., Burns J., Aziz A.A. Antioxidant avonols from fruits, vegetables and beverages: measurements and bioavailability. / Biol. Res, 2000; №33: P.79–88.
- 13. Shetty K. Role of proline-linked pentose phosphate pathway in biosynthesis of plant phenolics for functional food and environmental applications / A review. Process Biochem, 2004; №39: P. 789–803.

Received to editorial board 06.10.17

Я. Кавулич, асп., М. Кобилецька, канд. біол. наук, доц., О. Терек, д-р біол. наук, проф. Львівський національний університет імені І. Франка, Львів, Україна

ЗМІНА ВМІСТУ КСАНТОНІВ ТА НАГРОМАДЖЕННЯ ЛІГНІНУ В РОСЛИНАХ ГРЕЧКИ ТА ПШЕНИЦІ ЗА ДІЇ САЛІЦИЛОВОЇ КИСЛОТИ ТА ІОНІВ КАДМІЮ

Досліджено сумісний вплив іонів кадмію та саліцилової кислоти на вміст поліфенолів у рослинах гречки (Fagopyrum esculentum Moench.) і пшениці (Triticum aestivum L.). Встановлено, що за дії іонів кадмію зростає вміст ксантонів та посилено утворюється лігнін. Для зниження впливу стресового чинника доцільно використовувати саліцилову кислоту, яка нормалізує нагромадження фенольних сполук — вміст ксантонів та лігніфікацію у рослин гречки та пшениці. За допомогою цього регулятора росту можна певною мірою зменшити токсичний вплив іонів кадмію.

Ключові слова: Fagopyrum esculentum Moench., Triticum aestivum L., кадмію хлорид, саліцилова кислота, лігнін, ксантони.

Я. Кавулич, асп., М. Кобылецкая, канд. биол. наук, О. Терек, д-р биол. наук Львовский национальный университет имени Ивана Франко, Львов, Україна

ИЗМЕНЕНИЕ СОДЕРЖАНИЯ КСАНТОНОВ И НАКОПЛЕНИЕ ЛИГНИНА В РАСТЕНИЯХ ГРЕЧИХИ И ПШЕНИЦЫ ПРИ ДЕЙСТВИИ САЛИЦИЛОВОЙ КИСЛОТЫ И ИОНОВ КАДМИЯ

Исследовано совместное влияние ионов кадмия и салициловой кислоты на содержание фенолов (ксантонів, лигнина) в растениях гречихи (Fagopyrum esculentum Moench.) и пшеницы (Triticum aestivum L.). Установлено, что за действия ионов кадмия возрастает содержание ксантонов и усиленно образуется лигнин. Для снижения влияния стрессового фактора целесообразно использовать салициловую кислоту, которая нормализует содержание и снижает содержание ксантонов и лигнификацию в растениях гречихи и пшеницы. С помощью этого регулятора роста можно значительно уменьшить токсическое влияние ионов кадмия.

Ключевые слова: Fagopyrum esculentum Moench., Triticum aestivum L., кадмия хлорид, салициловая кислота, лигнин, ксантоны.

UDC 598.288.7:591.555.1

A. Markova, PhD stud., V.Serebryakov, SDc. Taras Shevchenko National University of Kyiv, Kyiv, Ukraine

DIFFERENCES IN AGGRESSIVE BEHAVIOR OF RELATED SPECIES OF FLYCATCHERS (MUSCICAPIDAE) FAMILY

The article is devoted to the observation of differences in relation between aggressive behavior of related species of Flycatchers (Muscicapidae) family and behavior acts in naturally watering places. Observations have reviled the timing separation between presence and engagement of Flycatchers in morning hours and relation with acts of aggression. Each representative of Flycatchers family is using the watering place in different ways. The correlation between intraspecific and interspecific contacts with the predominance of interspecific and highly aggressive interactions has been analyzed. The rating of successfulness of the acts of aggression has been established for every particular group of Flycatchers. It demonstrates the energetic justification of aggressive behavior for spotter, red-breasted and pied flycatchers but energetic overspend and failure for collared flycatcher.

Keywords: behavior, aggression, Muscicapidae, watering place.

Introduction. Over the last decade, interest to the fly-catcher's ecology significantly increased due to their synanthropic opportunities, habitat area expansion and population increasing in the southern Europe, as well as their relationships with the other species. For the social bird's interaction study, flycatchers are ideal species because some knowledge regarding the use of non-specific and cone-specific information in their choice of nesting place has already been partially disclosed. Besides these species are flexibly used an intraspecific and especially interspecific social information (for example, neighborhood with the great and the blue tits) [26].

Numerous publications of European authors, the question of the aggression's reasons and consequences among the animals are actively appeared. Especially essential attention is spared to behavior's differences investigation on different territories, its significance for biology, ecology and social relationships closed and competitive species. Much attention is paid to aggression study in intraspecific competition [14], but its significance and consequence in interspecific competition or other relationships of the closed species are the newer and not enough learnt issue so far [27, 36], but its mechanisms and consequences are still not clear.

Interspecific competition is an important factor which regulates niche overlapping in the resources use by the closed spices and relative density of the bird's population [38, 33]. Under natural conditions specimens of many spices are involved to this competition that certainly increases competition level and aggressive behavior as one of expression of competition [29].

Interspecific aggression has also an important consequence for ecological processes and provides with answers about the reasons of evolutional strategies behavior change. For today, there are still exist difficulties in understanding how exactly the behavior will influence on the structure, functions and stability of the ecosystem, interaction difficulties which exist between species and environment. Information exchange between specimens of the other species in relation to resources is extremely important and its mechanism may have impact to consistent patterns and consequences of species coexistence [21].

For forest and steppe zones of Ukraine breeding is spotted flycatcher (Muscicapa striata) and pied flycatcher (Ficedula hytoleuca) which are under protection of Bonn and Berne conventions and coralled flycatcher (Ficedula albicollis) and red-breasted flycatcher (Ficedula parva)

which have no environmental protection status but the number of which gradually decreased for the last years [11]. That's why flycatcher's ecological peculiarity and behavior study in Ukraine is extremely relevant which may help to keep them in the original habitats.

The purpose of this work is the investigation and interspecific (further InterS) ratios comparison and intraspecific (further IntraS) aggression for the four species of birds Muscicapidae family in the breading season at the natural watering place. The main objectives are:

- to detect the presence and significance of aggression with physiological needs which were determined according to the results of acts at the watering place and the presence and number of other species and their aggressiveness as a direct factor of aggression among flycatchers;
- to establish the justification of energy costs on aggressive behavior expression.

Methods and material. As materials served the data collected by the author in Kanev Nature Reserve (further KNR) of Cherkassy region in May and June 2010, 2012 and 2014 at the watering place in Mokry ravine in the household territory. Investigation territory has environmental protection status and it is characterized by the low anthropogenic influence. The total duration of observation in KNR is 324 hours. During this time about 1 324 interspecific and intraspecific contacts were fixed and 1 940 flycatchers' appearances were analyzed at the watering place.

Observations were conducted from 5.00 till 21.00 (hereinafter hours are corrected to daylight saving time). Light day period is conventionally divided into three periods: morning (from 5.00 till 12.00), day (from 12.00 till 17.00) and evening (from 17.00 till 21.00). Studying the dynamics of birds' activity at the watering places according to commonly applied ethological practices [1], possible variants of birds' behavior acts at the watering places were separated: water drinking, food consumption, bathing and cleaning feathers. Commonly applied ethological methods of "total observation" and "total record" [12] with author's modifications for birds observation in nature were applied to study interspecific behavior. Behavior act when two birds reduced the distance between them, obviously changing their

behavior compared to previous period of time, demonstrating readiness to attack and fight is considered to be an act of aggressive behavior [9].

Among the data, related to aggressive reaction, following information was recorded:

- which of species/specimen was the first who arrived the study area and which was the second one
- which of species/specimen showed initiative to aggression
- which of species/specimen won, i.e. stayed at the place of observation.

We counted the cases of winning the fight for resources having reached the place as the first one and cases of winning after having reached the place as a second one. Based on these data the distribution of specie's success rating in interspecific aggressive contacts was obtained.

Only the data collected taking into account same weather conditions is used for analysis. Statistical processing of the data is made applying mathematical methods using software Microsoft Excel and STATISTICA 7.0. The data is checked for normality, and, accordingly, correlation ratios were defined using parametric and nonparametric methods.

Study was performed as stage of research topic of Department of Zoology, NSC "Institute of Biology," Taras Shevchenko National University of Kyiv "Saving of the biodiversity and comprehensive study of adaptation strategies of phyto-, zoo- and virobioty of Ukraine using bio informational technologies, topic number 11BF036-02.

Results and discussion.

Dynamics of birds' engagement in behavioral acts at watering places. According to the type of food flycatchers are insectivorous birds [2, 5, 6, 7] and therefore their need for drinking is not so significant as the need of crops eating birds. So the main purpose of staying at watering place is cleaning feathers and bathing, although drinking and search for food still is a large share of behavioral acts at watering place. We identified maximum need of flycatchers for replenishment water balance in the body, bathing and search for food in different areas (Table 1).

Ficedula hypoleuca Ficedula parva **Peaks** Muscicapa striata Ficedula albicollis M D М D E M D М D Ε 12, 14 presence 6 14 20 8 12 18 6-7 19 8 12 17, 20 8 12 5, 9 13, 15 13 19 14-16 8 bathing 6 21 20 drinking 6 12 8 11 6 12 8 16 20 search for food 6 11 17 8 21 7, 9 18 6 16 20

Table 1. Peaks of engagement in behavioral acts at watering place during the day

Note: "M" - morning, "D" - day, "E" - evening, "-" - no visible peak

It was found out that biological needs of flycatchers at watering place are slightly separated in time. Especially important separation was noticed in morning hours. Maximum activity arrival of collared and red-breasted flycatchers was noticed at 8.00, and of pied and spotted flycatcher – at 6.00. It should be noted that that the place of research was selected given the lack of other sources of water. So the results about the separation of close species in time indicate ecological behavioral adaptation to limited resources. Besides, it indicated the choice of individual behavioral adaptation type. Collared and pied flycatchers have very similar ration and linear dimensions, but behavioral strategy of collared flycatcher is similar to behavior of spotted flycatcher, the number of which is large enough in the national park. In return, the behavior of pied flycatcher is similar to the behavior of red-breasted flycatcher. However, this trend may be wrong because the number pied flycatcher in recent years has decreased dramatically, and the species is not considered to be nesting in the area anymore.

Aggression and behavioral acts. Through the analysis of quantitative acts of aggressive behavior, the indexes of different behavior acts at the watering place for each species were defined (Table 2). Generally, the correlation between the appearance of individuals of their own species and aggressive reaction was noticed for all flycatchers. For collared and red-breasted flycatcher this correlation is average, and for pied and spotted flycatcher this correlation is low. Only for spotted flycatcher low correlation of aggressive behavior and overall increase of birds number and average correlation to increasing aggression of all birds at watering place was noticed. Besides, the watering place has its strategic importance for each species. Ration od the species is very similar during the nesting period and if the resource available is sufficient the birds do not compete [5]. But the watering place is one of the areas of food searching for the collared flycatcher, so due to the limited water resource nearby its competitive importance significantly increases. Banding in the ravine facilitates, to some extent, the search of flying insects because large specimens of butterflies and bees have often been meshed in the net for banding. Therefore, the correlation between the aggression and food searching at the watering place is high (r=0.842; p<0.01), and the correlation between the aggression and

drinking is lower, but still considerable. The watering place has more important role as a place of cleaning feather for the spotted flycatcher and as a source of after for the redbreasted flycatcher. The data for the pied flycatcher is still insufficient for specific conclusions.

Table 2. Relation between the aggression, behavioral acts and other birds on watering places

	Muscicapa striata	Ficedula albicollis	Ficedula hypoleuca	Ficedula parva
bathing	0.348*	-0.135	0.193	0.449*
drinking	-0.028	0.558*	0.229	0.436*
searching for food	0.115	0.842**	-0.111	-0.201
their kind	0.387*	0.489*	0.307*	0.544*
all birds	0.339*	-0.041	0.036	0.077
general aggression of birds	0.425*	-0.011	-0.032	0.217

Note: * p<0.05, ** p<0.01

Detailed research of the aggression of flycatchers with the presence of massive kinds of KNR on a watering place revealed a weak inverse correlation between the aggressiveness of the collared flycatcher and the number of the great tit, and the number and the aggressiveness of the blackcap. Instead, the connection between the aggressiveness of spotted flycatcher and the number and the aggressiveness of the great tit is direct and weak, but significant with the common chaffinch (with the quantity r=0.515; p<0.05 and the aggression r=0.504; p<0.05). The redbreasted flycatcher actively reacts on the aggressive behavior of the Eurasian blue tit (r=0.703; p<0.01), but weakly reacts on its number (r=0.413; p<0.05). An insignificant weak correlation is noticed between the pied flycatcher the aggressiveness of the robin, the great tit and the marsh tit.

In general, in recent years to determine the interconnection between the most explored types of the behavior the strength of correlations of different possible combinations of features was estimated by meta-analysis. Thus, based on data from 81 scientific works, the researchers found that the correlations between the behavior in general are weak and quite varied because of the variation of the comparable characteristics. The presence of partial correlation between features indicates that certain connections do not depend on covariance with other features, while some connections (in particular aggression or exploration of new territory) successively decrease after the controlling of covariance. At the same time, the magnitude of effects (eg. correlation) is systematically higher when behavior is

analyzed under the same experimental conditions. Differences in correlations arise not because of differences in recurrence, which are related to the measuring of different features, and most often assessed behavioral features do not necessarily form the same independent intervals (domains). Overall, between any behavioral acts there is a positive correlation of medium strength.

Data interpretation by such methods indicates that the recurrence research of certain behavioral acts is not statistically different, and their value influences more on correlations in the species-specific behavior than in the individual one [22]. Thus, the obtained data can be used to establish the behavioral plasticity of representatives of the Flycatchers.

Distribution of interspecific and intraspecific aggression. Interspecific relationships in a particular grouping of birds are closely related to intraspecific aggression of existing together species [3]. Usually, the number of interspecific contacts is considerably greater than intraspecific [4, 8, 10, 13]. We recorded species, to which flycatchers revealed the reaction of aggression for the whole time of observations (Table. 3). Thus, for the collared flycatcher among 19 species, that were encountered, there was an aggressive reaction to 9. The spotted flycatcher expressed an aggression to 7 out of 18 species, the pied flycatcher – to 2 out of 7, and the read-breasted flycatcher – to 1 out of 10. All flycatchers more frequently showed the reaction of aggression upon arrival at the watering place later than the object of attack.

Table 3. Species that are marked by the presence of aggressive behavior during interaction of species

Species	Muscicapa striata	Ficedula albicollis	Ficedula hypoleuca	Ficedula parva
Dendrocopos medius	-			
Dendrocopos minor	_			_
Hippolais icterina		+	_	_
Sylvia atricapilla	+	_	_	_
Phylloscopus collybita	-	_		_
Phylloscopus sibilatrix		+		
Muscicapa striata	+	_		
Ficedula parva	-	_	_	_
Ficedula hypoleuca	-	+	_	_
Ficedula albicollis	-	+		
Erithacus rubecula	+	1		
Turdus merula	_	1		
Turdus philomelos	+	1		
Parus caeruleus	+	-		_
Parus palustris	_	+		
Parus major	+	+	+	_
Sitta europaea	-	_		
Certhia familiaris	-	+	_	
Fringilla coelebs	+	+	+	+
Chloris chloris				_
Carduelis carduelis		_		
Coccothrausres coccothraustes	_	+		_

It is known that the amount of interspecific conflicts (aggressive contacts) in mixed populations is comparable to or greater than the frequency of intraspecific aggressive contacts [3]. These data are known for waterbirds, but this pattern was also confirmed for flycatchers (Table 4). It was established, that all four species of flycatchers pay a large share of attention to the interspecific aggressive interactions, but the percentage of intraspecific aggression

of the collared flycatcher is still higher than of the spotted one. The total share of interspecific contacts is bigger than intraspecific, that is associated to the high competition. This is especially expressed for small flycatchers. In turn, this confirms recent researches on active and flexible use of interspecies information and social relations of close and competitive species by flycatchers [26].

Table 4. Percentage of behavioral reaction to all species' contacts

	Muscicapa striata		Ficedula albicollis		Ficedula hypoleuca		Ficedula parva	
	InterS	IntraS	InterS	IntraS	InterS	IntraS	InterS	IntraS
Total number of contacts	84.29	15.71	75.39	24.61	69.39	30.61	91.67	8.33
Aggressive contacts	9.32	13.64	8.33	23.40	14.71	0	13.64	0
Non-aggressive contacts	90.68	86.36	91.67	76.60	85.29	100	86.36	100
Share or all aggressive contacts	78.57	21.43	52.17	47.83	100	0	100	0

Consequences of interspecific interaction, namely using the information, are asymmetric and they are used for interspecific coexistence modelling. Potential competitors are important component of efficient area use. Sometimes the presence of potential competitors even attracts birds [30, 31]. The more interspecific niches are overlapped, which is a case when the resource is limited, the better opportunities for using interspecific information appear, and strong competitors, for ensuring more accurate information [32, 35].

Importance of certain territory for territory species may depend not only on environment characteristics, but also on social structure of the area. Although interspecific competition can be asymmetric, as a rule it results in costs for all parties [19].

Protection of the territory is an energetically costly process [20], so keeping the information about territorial competitors and stable relationship is an additional advantage for the most part of birds. Birds often respond less aggressively to territorial specimen whom they often tolerate on their territory, than to distant neighbors or migratory birds [15, 16, 34, 37]. If the neighbors are less dangerous for secured recourses (food, individuals of their species, breeding), the respond is less aggressive in order to use as less energy as possible for accumulation of territorial competitiveness [19].

In our research the rating of pair aggressive contacts. It has no dimension but reflects the percentage of success (+) or loss (-) such interaction. Final calculation of results of flycatchers' pair collisions with each type separately indicates the competitive position of the flycatcher at some specific area (tab. 5). A sum of defense and attack indicates the overall justification of energy cost used for the competition and protecting the territory in a particular grouping of birds.

Table 5. Rating of aggressive contacts of Flycatchers

	Muscicapa striata	Ficedula albicollis	Ficedula hypoleuca	Ficedula parva
Attack	-1.63	-3.22	0.50	1
Defense	2.63	-0.78	2.50	1
Σ	1	-4	3	2

In the natural environment the collared and the spotted flycatchers typically have a low protection rating of an area, when they faced with a large number of other types of birds. This is due to the constant availability of the required resources. The same trend is noted for the collared flycatcher in case of an attack. Conversely, the spotted flycatcher is guite successful during attacks in pair interactions. However, for the pied and the red-breasted flycatchers, spending energy on aggression and attack protection is justified. As a result, there is rating of justification for energy costs of competitive aggression from the most depleted species of flycatchers - the collared flycatcher - to the most successful species - the red-breasted flycatcher. In summary, we note that flycatchers win the attack and lose protection, especially in contacts with the common chaffinch, the great tit and the blackbird.

This investigation reveals some possible scenarios of aggressive behavior on the ground watering to natural areas. Differences in flycatchers' participation in social interactions become more important in explaining adaptive individual differences in the behavior of animals and probably are part of the evolutionary process [17, 19]. Similar researches were performed in different areas and at different times on the example of European marmots. [25] Recent data regarding aggression among the greylag goose [39] also found that dominant behavior may depend not only on internal factors but also on the season and social environment. In addition, the best choice to achieve or maintain a high ranking domi-

nation can vary significantly between the stages of the life cycle. This highlights the importance of long-term research and multivariate approaches for understanding the complexity of the relations of domination for animals.

Overall, there is an individual right behavioral response of a group of individuals to external signs and the type of behavior of its species. For ethological studies such signs serve as a key to understanding behavioral ecology and quantitative genetics. Interaction between individuals (social conditions) is a major factor in changing behavioral variations at different levels of the hierarchy [18]. Social interactions lead to a restructuring of complex behaviors and tend to occur at the level of the group. This mechanism of behavioral change strategies has unknown evolutionary consequences, justifying its study.

Conclusions:

- 1. Detected distribution in time of occurrence flycatchers at the watering place during the day. A special feature is the morning dynamics of species: the collared and the redbreasted flycatchers actively visit the watering place at 8 am, and the pied and the spotted flycatchers at 6 o'clock.
- 2. The spotted flycatcher's aggression correlate with the general level of birds' aggression and for the collared, the red-breasted and the pied flycatchers correlation is only available with the advent of their species in the natural environment and of the need for resources.
- 3. Have been revealed that in the ratio of interspecific and intraspecific contacts prevail aggressive interspecific

interactions, indicating the importance of establishing an interspecific hierarchy for flycatchers and active use of interspecific information.

- 4. Aggressive interactions for the collared flycatcher are the most debilitating and energy unjustified. Most energetically justified is the interaction of the red-breasted and the pied flycatchers in the reactions of protection and attack on the watering place. The spotted flycatcher occupies an intermediate position in the ranking of success at the natural watering places in Kanev Nature Reserve.
- 5. Obtained data in respect of the distribution of the flycatchers' aggressive behavior complement the already known knowledge and point to the diversity of behavioral strategies of birds of one family. Basic mechanisms and causes of differences have still needed further investigation.

- 1. Аманова М.А. К характеристике ритма прилета птиц на водопой в условиях пустыни / М.А. Аманова // Мат-лы IV Всесоюзная орнитологичная конференция. - Алма-Ата. 1965. - С. 9-10.
- 2. Егорова Г.В. Сравнительная экология близкородственных видов мухоловок рода Ficedula / Г.В Егорова, А.Е. Иванов, В.М Констан-
- тинов М.: ФГОУ-ВПО-МГАВМиБ имени К. И. Скрябина, 2007. 179 с.

 3. Иваницкий В.В. Этологические аспекты взаимоотношений между близкими видами животных / В.В. Иваницкий // Зоологический журнал. – 1982. – Т. 61, Вып. 10. – С. 1461–1471.
- 4. Иванницкий В.В. Межвыдовые отношения симпатрических видов каменок (Oenanthe, Turdidae, Passeriformes). Поведенческие аспекты сосуществования близких видов / В.В. Иванницкий // Зоологический журнал. – 1980. – Т. 59., № 5. – С. 739–749.
- Иванов А.Е. Экология близкородственных видов мухоловок рода Ficedula в местах их симбиотопии / А.Е. Иванов // Русский орнитологический журнал. – 2006. – Т. 13, Вып. 351. – С. 87–94.
- 6. Марисова И.В. К биологии мухоловки-белошейки (Muscicapa albicolis Temm.) в западных областях Украины / И.В. Марисова, Н.М. Холина // Фауна и животный мир советских Карпат. – Ужгород, 1959. – T. 40. – C. 75–81.
- 7. Марочкина Е.А. Индивидуальные особенности питания и поведения серых мухоловок Muscicapa striata / Е.А. Марочкина, А.В. Барановский., С.И. Ананьева [и др.] // Русский орнитологический журнал. – 2005. – Т. 14, Вып. 296. – С. 744–748.
- 8. Панов Е.Н. Межвидовые территориальные отношения в смешанной популяции чернобокой каменки Oenanthe finchi и каменки-плешанки *O. pleschanka* на полуострове Мангышлак / Е.Н Панов, В.В. Иваницкий // Зоологический журнал. – 1975. – Т. 54, № 9. – С. 1357–1370.
- 9. Панов Е.Н. Механизмы коммуникации у птиц / Е. Н Панов. М.: Наука, 1978. - 304 с.
- 10. Панов Е.Н. Пространственные взаимоотношения четырех видов сорокопутов в Южной Туркмении / Е.Н Панов, В.В. Иваницкий // Зоологический журнал. – 1979. – Т. 58, № 10. – С. 1518–1535.
- 11. Пернаті друзі. Пташиний світ України. http://pernatidruzi.org.ua/ art.php?id=565
- 12. Попов С.В. Методические рекомендации по этологическим наблюдениям за млекопитающими в неволе / С.В. Попов, О.Г. Ильченко // М.: Московский зоопарк, 2008. – 165 с.
- 13. Рябицев В.К. Результаты исследования межвидовых территориальных отношений птиц на Южном Ямале / В.К. Рябицев // Зоологический журнал. – 1977. – Т. 56, № 2. – С. 232–242.
- 14. Arnott G. Assessment of fighting ability in animal contests/ G. Arnott, R.W. Elwood // Animal Behaviour. 2009. Vol. 77. P. 991–1004.
- 15. Briefer E. When to be a dear enemy: flexible acoustic relationships of neighbouring skylarks, Alauda arvensis / E. Briefer, F. Rybak, T. Aubin // Animal Behaviour. - 2008. - Vol. 76. - P. 1319-1325.
- 16. Brunton D.H. A test of the dear enemy hypothesis in female New Zealand bellbirds (*Anthornis melanura*): female neighbors as threats / D.H. Brunton, B. Evans, T. Cope [et.al.] // Behavioral Ecology. – 2008. – Vol. 19. – P. 791–798.
- 17. Colléter M. Personality traits predict hierarchy rank in male rainbowfish social groups / M. Colléter, C. Brown // Animal Behaviour. - 2011. -Vol. 81, № 6. – P. 1231–1237.
- 18. Dingemanse N.J. Interacting personalities: behavioural ecology meets quantitative genetics / N.J. Dingemanse, Y.G. Araya-Ajoy // Trends in Ecology and Evolution. – 2015. – Vol. 30, № 2. – P. 88–97.

 19. *Dingemanse* N.J. The relation between dominance and exploratory
- behavior is context-dependent in wild great tits / N.J. Dingemanse, P. de Goede // Behavioral Ecology. - 2004. - Vol. 15, № 6. - P. 1023-1030.
- 20. Eason P. New birds on the block-new neighbors increase defensive costs for territorial-male willow ptarmigan / P. Eason, S.J. Hannon
- // Behavioral Ecology and Sociobiology. 1994. Vol. 34. P. 419–426.
 21. Forsman J.T. Competitor density cues for habitat quality facilitating habitat selection and investment decisions / J. T. Forsman, M.B. Hjernquist, J. Taipale [et.al.] // Behavioral Ecology. – 2007. – Vol. 19, № 3. – P. 539–545.
- 22. Garamszegi L.Z. A meta-analysis of correlated behaviors with implications for behavioral syndromes: relationships between particular behav-

- ioral traits / L.Z. Garamszegi, G. Markó, G. Herczeg // Behavioral Ecology. -
- 2013. Vol. 24, № 5. P. 1068–1080. 23. Grether G.F. The role of interspecific interference competition in character displacement and the evolution of competitor recognition / G.F. Grether, N. Losin, C.N. Anderson [et. al.] // Biological Reviews. – 2009. – Vol. 84. – P. 617–635.
- 24. Grether, G.F. The evolutionary consequences of interspecific aggression / G.F. Grether, C.N. Anderson, J.P. Drury [et. al.] // Annals of the New York Academy of Sciences. - 2013. - Vol. 1289. - P. 48 -68.
- 25. Hewitt S.E. Context-dependent linear dominance hierarchies in social groups of European badgers, *Meles meles /* S.E. Hewitt, D.W. Macdonald, H.L. Dugdale // Animal Behaviour. 2009. Vol. 77, № 1. – P. 161–169.
- 26. Jaakkonen T. The use and relative importance of intraspecific and interspecific social information in a bird community / T. Jaakkonen, S.M. Kivelä, C. M. Meier [et. al.] // Behavioral Ecology. - 2014. - Vol. 26, N 1.
- 27. Lehtonen T.K. Territorial aggression can be sensitive to the status of heterospecific intruders / T.K. Lehtonen, J.K. McCrary, A. Meyer // Behavioral Processess. – 2010. – Vol. 84. – P. 598–601.
- 28. Martin P.R. Ecological and fitness consequences of species coexistence: a removal experiment with wood warblers / P.R. Martin, T.E. Martin // Ecology. - 2001. - Vol. 82. - P. 189-206.
- 29. Mikami O.K. Does interspecific territoriality reflect the intensity of ecological interactions? A theoretical model for interspecific territoriality / O.K. Mikami, M. Kawata // Evolutionary Ecology Research. - 2004. - Vol. 6. P. 765–775.
- 30. Mönkkönen M. Heterospecific attraction among forest birds: a review. / M. Mönkkönen, J.T. Forsman // Ornithological Science. 2002. Vol. 1. – P. 41–51.
- 31. Mönkkönen M. Numerical and behavioural responses of migrant passerines to experimental manipulation of resident tits (Parus spp.): heterospecific attraction in northern breeding bird communities? / M. Mönkkönen, P. Helle, K. Soppela // Oecologia. - 1990. - Vol. 85. - P. 218-225.
- 32. Parejo D. The heterospecific habitat copying hypothesis: can competitors indicate habitat quality? / D. Parejo, E. Danchin, J. Aviles // Behavioral Ecology. 2005. Vol. 16. P. 96–105.
- 33. Peiman K.S. Ecology and evolution of resource -related heterospecific aggression / K.S. Peiman, B.W. Robinson // Quarterly Review of
- Biology. 2010. Vol. 85. P. 133–158. 34. Rosell F. Territory ownership and familiarity status affect how much male root voles (Microtus oeconomus) invest in territory defence / F. Rosell, G. Gundersen, J.F. Le Galliard // Behavioral Ecology and Sociobiology. – 2008. – Vol. 62. – P. 1559–1568.
- 35. Seppänen J.T. Social information use is a process across space, time and ecology, reaching heterospecifics / J.T. Seppänen, J.T. Forsman, M. Mönkkönen [et. al.] // Ecology. - 2007. - Vol. 88. - P. 1622-1633.
- 36. Tanner C.J. To fight or not to fight: context-dependent interspecific aggression in competing ants / C.J. Tanner, F.R. Adler // Animal Behavioral. - 2009. – Vol. 77. – P. 297–305. 37. Temeles E.J. The role of neighbors in territorial systems-when are
- they dear enemies / E.J. Temeles // Animal Behaviour. 1994. Vol. 47. P. 339-350.
- 38. Umapathy G. The occurrence of arboreal mammals in the wet evergreen forests of the Anamalai hills in the Western Ghats, South India / G. Umapathy, A. Kumar // Biological Conservation. - 2000. - Vol. 92. -P. 311-319.
- 39. Weiß B.M. A longitudinal study of dominance and aggression in greylag geese (Anser anser) / B.M. Weiß, K. Kotrschal, K. Foerstera // Behavioral Ecology. - 2011. - Vol. 22, № 3. - P. 616-624.

References (Scopus)

- Amanova MA. [To description of rhythm of arriving of birds on watering in the conditions of the desert]. Materials of the IV All-union ornithologicalconference; Alma-Ata; 1965. p. 9–10. Russian.

 2. Egorova GV, Ivanov AE, Konstantinov VM. Sravnitel'naja jekologija
- blizkorodstvennyh vidov muholovok roda Ficedula M.: FGOU-VPO-MGAVMiB imeni K. I. Skrjabina, 2007. 179 s. Russian
- 3. Ivanitskiy V.V. (1982) [Ethological aspects of relationship between close animal species]. Zoological journal. 1982;61(10):1461-1471. Russian.
- 4. Ivannitskiy VV. (1980) [Interspesific relationship sympatric species heaters (Oenanthe, Turdidae, Passeriformes). The behavioral aspects of coexistence of similar species]. Zoological journal. 1980;59(5):739-749. Russian.
- 5. Ivanov A. E. Jekologija blizkorodstvennyh vidov muholovok roda Ficedula v mestah ih simbiotopii. Russian ornithological journal. 2006;13(351):87-94. Russian.
- Marisova IV, Holina NM. [On the biology of collared flycatcher (Muscicapa albicollis Team.) in the western regions of Ukraine]. Flora and
- fauna of the Soviet Carpathians. Uzhgorod, 1959:40:75–81. Russian.
 7. Marochkina EA, Baranovskiy AV, Ananeva SI, et. al. [Individual feeding habits and behavior of spotted flycatcher Muscicapa striata]. Russian ornithological journal. 2005;14(296):744–748. Russian.
- 8. Panov EN, Ivanitskiy VV. [The interspecific territorial relations in the mixed population of Finsch's Wheatear Oenanthe finchi and pied wheatea O.pleschanka on the peninsula of Mangyshlak]. Zoological journal. 1975;54(9):1357-1370. Russian.
- Panov EN. [Mechanisms of communications in birds]. Moscov: Science. 1978. 304 p.

- 10. Panov EN, Ivanitskiy VV. [Spatial relationship of four types of shrikes in the Southern Turkmenistan]. Zoological journal. 1979;58(10):1518-1535. Russian.
- 11. Feathered friends. Avian Ukraine world. [http://pernatidruzi.org.ua/art.php?id=565]. Ukrainian.
- 12. Popov SV, Ilchenko OG. [Methodical recommendations about ethological supervision over mammals in slavery]. Moskov: Moskovskiy zoopark, 2008.165 p. Russian.
- 13. Ryabitsev VK. [Results of research of the interspecific territorial relations of birds on the Southern Yamal]. Zoological journal. 1977;56(2):232–242. Russian.
- Arnott G, Elwood RW. Assessment of fighting ability in animal contests. Animal Behaviour. 2009;77:991–1004.
 Briefer E, Rybak F, Aubin T. When to be a dear enemy: flexible
- 15. Briefer E, Rybak F, Aubin T. When to be a dear enemy: flexible acoustic relationships of neighbouring skylarks, *Alauda arvensis*. Animal Behaviour. 2008;76:1319–1325.
- 16. Brunton DH, Evans B, Cope T, et.al. A test of the dear enemy hypothesis in female New Zealand bellbirds (*Anthornis melanura*): female neighbors as threats. *Behavioral Ecology*. 2008;19:791–798.
- 17. Colléter M, Brown C. Personality traits predict hierarchy rank in male rainbowfish social groups. Animal Behaviour. 2011;81(6):1231–1237.

 18. Dingemanse NJ, Araya-Ajoy YG. Interacting personalities:
- 18. Dingemanse NJ, Araya-Ajoy YG. Interacting personalities: behavioural ecology meets quantitative genetics. Trends in Ecology and Evolution. 2015;30(2):88–97.
- 19. *Dingemanse* NJ, de Goede P. The relation between dominance and exploratory behavior is context-dependent in wild great tits. Behavioral Ecology. 2004;15(6):1023–1030.
- 20. Eason P, Hannon SJ. New birds on the block-new neighbors increase defensive costs for territorial-male willow ptarmigan. Behavioral Ecology and Sociobiology. 1994;34:419–426.
- 21. Forsman JT, Hjernquist MB, Taipale J, et.al. Competitor density cues for habitat quality facilitating habitat selection and investment decisions. Behavioral Ecology. 2007;19(3):539–545.
- Garamszegi LZ, Markó G, Herczeg G. A meta-analysis of correlated behaviors with implications for behavioral syndromes: relationships between particular behavioral traits. Behavioral Ecology. 2013;24(5):1068–1080.
 Grether GF, Losin N, Anderson CN, et. al. The role of interspecific
- Grether GF, Losin N, Anderson CN, et. al. The role of interspecific interference competition in character displacement and the evolution of competitor recognition. Biological Reviews. 2009;84:617–635.
- 24. Grether GF, Anderson CN, Drury JP, et. al. The evolutionary consequences of interspecific aggression. Annals of the New York Academy of Sciences. 2013;1289:48–68.
- 25. Hewitt SE, Macdonald DW, Dugdale HL. Context-dependent linear dominance hierarchies in social groups of European badgers, *Meles meles*. Animal Behaviour. 2009;77(1):161–169.

- 26. Jaakkonen T,. Kivelä SM, Meier CM, et. al. The use and relative importance of intraspecific and interspecific social information in a bird community. Behavioral Ecology. 2014;26(1):55–64.
- Lehtonen TK, McCrary JK, Meyer A. Territorial aggression can be sensitive to the status of heterospecific intruders. Behavioral Processess. 2010;84:598–601.
- 28. Martin PR, Martin TE. Ecological and fitness consequences of species coexistence: a removal experiment with wood warblers. Ecology. 2001;82:189–206.
- 29. Mikami OK, Kawata M. Does interspecific territoriality reflect the intensity of ecological interactions? A theoretical model for interspecific territoriality. Evolutionary Ecology Research. 2004;6:765–775.
- 30. Mönkkönen M, Forsman JT. Heterospecific attraction among forest birds: a review. Ornithological Science. 2002;1:41–51.
- 31. Mönkkönen M, Helle P, Soppela K. Numerical and behavioural responses of migrant passerines to experimental manipulation of resident tits (*Parus* spp.): heterospecific attraction in northern breeding bird communities? Oecologia. 1990;85:218–225.
- 32. Parejo D, Danchin E, Aviles J. The heterospecific habitat copying hypothesis: can competitors indicate habitat quality? Behavioral Ecology. 2005:16:96–105.
- 33. Peiman KS, Robinson BW. Ecology and evolution of resource related heterospecific aggression. *Quarterly Review* of *Biology*. 2010;85:133–158.
- 34. Rosell F, Gundersen G, Le Galliard JF. Territory ownership and familiarity status affect how much male root voles (*Microtus oeconomus*) invest in territory defence. Behavioral Ecology and Sociobiology. 2008;62:1559–1568.
- 35. Seppänen JT, Forsman JT, Mönkkönen M, et. al. Social information use is a process across space, time and ecology, reaching heterospecifics. Ecology. 2007;88:P. 1622–1633.
- Tanner CJ, Adler FR. To fight or not to fight: context-dependent interspecific aggression in competing ants. Animal Behavioral. 2009;77:297–305.
- 37. Temeles E.J. The role of neighbors in territorial systems when are they dear enemies. Animal Behaviour. 1994;47:339–350.
- 38. Umapathy G, Kumar A. The occurrence of arboreal mammals in the wet evergreen forests of the Anamalai hills in the Western Ghats, South India. Biological Conservation. 2000;92:311–319.
- 39. Weiß BM, Kotrschal K, Foerstera K.A longitudinal study of dominance and aggression in greylag geese (*Anser anser*). Behavioral Ecology. 2011;22(3):616–624.

Received to editorial board 14.12.16

А. Маркова, асп., В. Серебряков, д-р біол. наук Київський національний університет імені Тараса Шевченка, Київ, Україна

ВІДМІННОСТІ У ПРОЯВІ АГРЕСІЇ БЛИЗЬКИМИ ВИДАМИ РОДИНИ МУХОЛОВОК (MUSCICAPIDAE)

Робота присвячена вивченню відмінностей зв'язку агресивної поведінки близьких видів родини Мухоловкові (Muscicapidae) із поведінковими актами на водопої у природі. Виявлено розподіл у часі присутності та зайнятості мухоловок у ранкові години та зв'язок із проявом агресії. Кожен із представників мухоловок використовує водопій по-різному. Розглянуто співвідношення міжвидових та внутрішньовидових контактів, серед яких переважають міжвидові, особливо агресивні, взаємодії. Встановлено рейтинг успішності прояву агресії мухоловками у конкретному угрупованні. Він вказує на енергетичну виправданість агресивної поведінки для сірої, малої та строкатої мухоловки, але максимальну затратність та програш для мухоловки білошиї.

Ключові слова: поведінка, агресія, Muscicapidae, водопій.

А. Маркова,асп., В.Серебряков, д-р. биол. наук Киевский националый университет имени Тараса Шевченко, Киев, украина

ОТЛИЧИЯ В ПРОЯВЛЕНИИ АГРЕССИИ БЛИЗКИМИ ВИДАМИ СЕМЕЙСТВА МУХОЛОВКОВЫЕ (MUSCICAPIDAE)

Работа посвящена изучению отличий между связью агрессивного поведения близких видов семейства Мухоловковых (Muscicapidae) и поведенческими актами на водопое в природе. Выявлено разделение во времени присутствия и занятости мухоловок в утренние часы и связь с проявлением агрессии. Каждый из представителей мухоловок использует водопой по-разному. Рассмотрены соотношения межвидовых и внутривидовых контактов, среди которых преобладают межвидовые, особенно агрессивные, взаимодействия. Установлен рейтинг успешности проявления агрессии мухоловками в конкретной среде обитания. Он указывает на энергетическую оправданность агрессивного поведения для серой, малой и пестрой мухоловки, но максимальную затратность и проигрыш для мухоловки-белошейки.

Ключевые слова: поведение, агрессия, Muscicapidae, водопой.