

We are IntechOpen, the world's leading publisher of Open Access books Built by scientists, for scientists

6,900

Open access books available

186,000

International authors and editors

200M

Downloads

Our authors are among the

154

Countries delivered to

TOP 1%

most cited scientists

12.2%

Contributors from top 500 universities



WEB OF SCIENCE™

Selection of our books indexed in the Book Citation Index
in Web of Science™ Core Collection (BKCI)

Interested in publishing with us?
Contact book.department@intechopen.com

Numbers displayed above are based on latest data collected.
For more information visit www.intechopen.com



Conspecific Recognition Systems and the Rehabilitation of the Biological Species Concept in Ornithology

V. S. Friedmann

Additional information is available at the end of the chapter

<http://dx.doi.org/10.5772/53496>

1. Introduction

The species problem, as it has been discussed by zoologists for over a hundred years, is formed by two aspects. On the one hand, there is an objective controversy, a kind of a gap, between species as they actually exist in nature and the 'classifier's species' identified by a group-expert taxonomist; on the other hand, there is everyone's natural aspiration to identify the species in accordance with nature, to purposefully narrow this gap, and ideally, to close it completely. [15, 9, 43]. One of the creators of the modern evolutionary synthesis, N. V. Timofeeff-Ressovsky had good grounds for considering the notion of discreteness of life to be the crucial part of biological thinking, i.e. the idea of particulate essence of biodiversity. In other words, life-forms don't flow into one another smoothly and gradually, but rather are divided into units, partly totally discreet, partly connected with transitional forms – the ones that haven't separated completely.

Being included into such a group as species proves to be important for the specimens it comprises. It is even more important than the individual survival and reproduction, primarily because an individual can't improve its adjustment alone, but only in association with the others within a species-specific pattern of relations (to the territory, as well as social, habitat and other relations) in the superindividual population system [55, 57-58, 10]. To this end, specimens competing with each other for a territory and a mate invest their energy into the long-term reproduction of the specific pattern of spacial-ethological structure of the population, and simultaneously try to occupy the best position in this structure of relations within one of the population groups. It can be a dominant status in the community structured by the hierarchy (based on the agonistic dominance), taking of the best territories for territorial

species (where their 'quality' is defined by the position in the anisotropic space of the group and by an earlier time of acquisition), attraction of a greater number of 'better quality' partners, and so on [58, 11-12].

Anyway, achieving superiority over the others (distribution in space or in mosaic habitats, and other homologous processes) through the competitive social communication within the species-specific relations allows the individual to exploit those relations more effectively as a resource of even more superiority and/or maximising the individual's final adjustment.

The latter can be understood differently: as an advantageous (in comparison with other specimens that have chosen alternative strategies) replication of the individual's progenies or genes. In any case, being bound by specific relations to the others within the superindividual population system and a more effective maintenance of these relations, both are crucial for the individual's successful struggle for survival [10-11]. And consequently, for the distribution of life strategies carried by the successful individuals. At present this 'morphological' understanding of a population is just beginning to form; the view of population as an integral system characterised by a pattern of relations that are consistently reproducible in the sequence of generations in the stochastics of collisions and interactions of specimens [10].

Accordingly, separate individuals with their activeness, adjustment and destiny here are only a means to identify the most effective set of life strategies and configuration pattern of spatial-ethological structure of the system in the direction of its most sustainable / long-term reproduction (given the local features of external 'perturbations' of the ecological environment and the demographic 'tension' within the system).

We are mentioning this understanding of population for two reasons. First, it surprisingly consorts with Vavilov's understanding of species (an essential part of the biological species concept) as a system of populations that interact in a particular area. And inter alia regulate redistribution of individuals in the mosaic habitats to maintain integrity in the system and maximize its reproductive output (despite the demographic randomness and environmental instability).

Secondly, it follows that the key moment of an elementary evolutionary phenomenon - the isolated process of selective changes in biological form, which make up everything, including the formation of species, is not in itself the victory of the individual over another in the struggle for existence. This inclusion (or exclusion, fragile, unstable inclusion, acceptance on the "worst position") in the form specific to spatial-ethological structure of populations. Only this makes it possible to maximize the fitness of individuals in competition with each other, but only within the processes of social communication, structured in accordance with the specific "rules of the game", where "errors" or "fraud" exclude the specimens from the system [11, 19].

This means that the 'friend-foe' recognition within the corresponding interactions, especially when the individual is included in the system of relations inside the species population, is important for maintaining the integrity in the species ("Vavilov's species", which is the most consistent with the "species in nature", if we adhere to the population approach versus the typological one). Further on we will discuss what means of intersystem regulation are used

to perform this task; while here we shall note that this very same 'friend-foe' recognition will naturally maintain the isolation of the species where the nature "puts it to a test". For example, in the areas of secondary contact with hybridization, where the isolating mechanisms are not yet developed [49] and/or existing obstacles for cross-breeding are insufficient, but are not perfected by selection [53], nevertheless the isolation of forms remains without a 'blur' [1, 7, 24, 50].

2. Population as a system and «the species problem»

This results in our hypothesis that the integrity of population subunits within the species and its isolation from close forms outside are supported by the same in-system regulation mechanism related to the directional selection of the specimens between groups by the potentialities of development of certain behaviors, or by the selection of one of the alternative strategies in a particular environment. As the author is an ornithologist, the examples and argumentation are taken mainly from the ornithological material, but in such a way that they could be used as the basis for general theoretical propositions. The more so because a significant difference between the taxon of birds and other macrotaxa is that the description of its structure of biodiversity (in the interpretation of A.A.Nazarenko [42]) is overall complete [18, 40]. Already, the changes in the numbers of bird species are more due to the change of the prevailing concepts of species and/or concepts of speciation in the scientific community, rather than to the discovery of new forms [1, 32, 65].

Directional migration of non-resident specimens between groups, which connect the network of settlements scattered or isolated from each other on the "islands" of habitats, have been described recently and are just beginning to be studied [10-12]. It becomes clear that they are capable of directional redistribution of individuals from "reserve"¹ to restore species population that has declined locally due to a depression of internal nature, extermination or a natural disaster. These mechanisms work quite accurately both in respect of the population size, correlated with the capacity of "vacant" habitats, and of the spatial-ethological structure of newly created settlements, correlated with species-specific "ideal model" of the latter. The most important work here was done by N.A.Shchipanov [57-58] on the functional structure of the populations of small mammals and Y.P.Altukhov [2] on the intra- and inter-population regulation of the optimal level of gene frequencies through differential dispersion of different genotypes.

On the other hand, it has been shown (mainly for birds and mammals, but also for juvenile freshwater fish — [48]) that the flow of the dispersion of individuals within a population, whether the dispersion of the young or the resettlement of the adult

¹ the composition of the latter is extremely heterogeneous (e.g., [57-58]). On the one hand, these are all kinds of "losers" in the competition, who have lost their territory and/or a partner because of the inefficiency of behavior, the wrong choice of life strategy, etc., or non-territorial vagrant individuals that had never had either. On the other hand — they are the deported from areas where the species habitat had been destroyed by a local disaster, such as fire, floods, deforestation, etc. On the third — they are, on the contrary, the "best" specimens, the winners of the competition in their own group, relocating to another, "better" one to maximize their reproductive success (on these directed migrations see [11]).

- a. are directed and not random;
- b. are predetermined not so much by "guide lines" of environmental or landscape character, or gradients of habitat change within the area, as by the anisotropy in the position of different groups in the "network" of the species' settlements in the corresponding area, the presence of the "best" (stable / large) and "worst" (unstable, more temporary and small) groups, between which the streams of migrants are moving. From the first to the second evict mostly unsuccessful individuals displaced from the "best" neighborhoods, characterized by higher density and more intense competition for territory and / or a partner; in the opposite direction — their antagonists that increase their reproductive success by resettlement [20, 36, 12];
- c. the sustainable reproduction of populations of different levels, from local communities (demes) to geographic populations and, most likely, subspecies too is more dependent on constant influx of immigrants from the outside than on the efficiency of the residents' breeding [11, 59]. In any case, it has been shown for different species that the reduction of the flow while keeping the average (or even higher) level of breeding success of residents leads to a directed decline in population size and invariably leads to extinction sooner or later, unless the flow is restored. Therefore, species are so vulnerable to fragmentation of the natural landscape, the isolation of settlements in the emerging "islands" [59, 57]. Particularly vulnerable are those with underdeveloped "restoration" subsystem of the population system, a "reserve" of non-resident specimens is small and inactive, and the residents adhere to the K-strategy, are firmly tied to the social partners, territories and/or habitats [57, 11].

In other words, connectivity of territorial divisions "within" the system, its ability to "manage" the movements and interactions of individuals in a wide range is more important for population viability than breeding efficiency in local groups. Therefore, factors, processes and mechanisms that improve intrasystemic regulation, increasing the stability and direction of migration of individuals between groups, "in terms of" natural selection have an advantage over local adaptations;

- d. the settlement of individuals within an area by no means eliminates morphobiological differences between populations or lead them to a certain common denominator. On the contrary, it *enhances them*, because happens asymmetrically and includes a "sorting" of specimens by the potentialities of different behavioral / life strategies that exist within the area [10, 12].

So it is quite a common situation when a more than significant intraspecific differentiation of forms (based only on their degree of morpho-ecological divergence they could be considered a separate species) is achieved not through isolation, but while maintaining sustainable exchange of specimens with the rest of populations of the species. An example is a resident endemic form of the Albion Mountains crossbill in southern Idaho, which coevolved together with the lodgepole pine *Pinus contorta lafifolia*. Analysis of amplified fragment length polymorphism (method AFLP) showed a divergence of about 5% of loci, despite the existence of a stable gene exchange with other forms of this species. A similar pattern is shown

for nine more forms in a group of common crossbills *Loxia curvirostra* in North America, complex for a taxonomer as they have significantly diverged morphologically, and in the vocalization type [46]. Examples of this are plentiful ([14] and others).

It is now clear that the morphological, ecological, and genetic divergence of intraspecific forms, including reaching the level of "good species" does not require isolation and disjunction of the range, but is achievable also when a binding flow of genes is present. The movements of individuals controlling it are not homogenizing, but differentiating for the subunits of a population system [10, 12].

Conclusions **a–d** bring us back to the subject of the work - the system of 'friend-foe' recognition as a key to the renaissance of the biological species concept. Based on the systemic understanding of the population and the "morphological approach" to the population structure and dynamics, we can rectify the main disadvantage of using the biological species concept at the peak of its popularity in zoology in 1960-1970's, associated with the inconsistency in the conduct of its main principles — "species differ not by differences [in character] but by isolation [of population systems of different forms from each other]". See [21, 34, 52].

The more so because among biologists, at least among evolutionists, there aren't any discrepancies in relation to "what is population is". In evolutionary biology, population is the only subject of evolution, and its specimens are real carriers both of "standard development" programs and evolutionary innovations" [42: 181]. considering the current dissonance of ideas about what species actually is (even in theory), this uniformity in respect of population approach may be a common basis for the definition of "species in nature", and a directed movement towards them from the "taxonomer's species".

Unfortunately, routinization in the practical application of the concept has led to the fact that the required 'isolation' is understood solely as a reproductional discreteness of form — sterility or other inferiority of hybrids in respect of fertility/survival, bringing to life the "selection against hybrids". If at the beginning of hybridization they do not exist, selection, aimed at preserving the locally co-adapted gene complexes, "perfects" the isolating mechanisms, which promotes the establishment of the required discreteness [34, 44, 52]. We shall see that the "conservation" and "perfection" must be taken into question.

3. Completion of speciation "natural experiments"

First, they are the different scale disjunction of areas, the number associated with depression in population, man-made, climatic and other environmental changes, ranging from short to encompassing historical time scales. Second, they are the hybridization in the zones of secondary contact with similar forms, long-term and regular enough, that there arise fully hybridogeneous populations or at least containing a significant fraction of hybrids. The change in population of a species in response to the former shows integrity and connectivity of territorial elements of its population system, the latter — its isolation from the population systems of other species with which this one hybridizes. In fact, "isolation" in Ernst Mayr's

understanding is one aspect of the modern population concept that assumes a well-defined system² characterized by a specific pattern of structure and the ability to consistently reproduce the species-specific morphotype and a pattern of spatial-ethological structure of the species population despite various "tensions" inside and "disturbances" from the outside. Even as powerful as a steady, long-term gene flow across the hybrid zone.

Therefore, the "morphological approach" is as productive in relation to population system of the species, as to the species morphotype. On the basis of it, the isolation of the species level is understood as the ability of the population system to stably reproduce the specific type (which includes not only the biology, but any specific pattern of ecological, behavioral traits, etc.), and the specificity of the population structure in spite of the two main types of "disturbances" mentioned above. Then the results of the two "natural experiments" provide an objective and complete test for the evaluation of "speciesness" of this form.

It follows that the "nature-friendly" species concept, aimed at defining the "species in nature", must follow the events and situations in which individuals of the two different forms (for which a taxonomist doubts whether they have reached the species level of divergence or not) manifest their own specific isolation separating themselves from the "foes". Or, conversely, "refute" it, merging with them in a single group or forming a series of transitional forms. This, of course, is not a rare event and individual "mistakes", but the bulk of population processes purposefully unfolding before the researcher.

Fortunately, the natural processes of areas dynamics — environmental, demographic, etc. — always create both types of "test cases". And they need to be used to test and improve the species concepts we use, as well as to refute the hypothesis about the status of these forms (for any taxonomer's propositions are hypotheses, [47]).

The biological species concept has not been able to explain some of the results of both "natural experiments". Among them:

- a. persistence of the isolation of forms in the presence of a long-standing and stable gene flow between them, so that gene pools are long and well blended. Given that the improvement of the isolation mechanisms by selection is not observed either, hybridization in contact zones takes place unobstructed, without any assortative mating at all, or with an insufficient and a constant level of assortativeness [43, 50, 51]. These are classic examples of zones of secondary contact with hybridization: gray and black crows in Europe and Asia; three forms of northern flickers in North America (*Colaptes (auratus?) auratus, cafer* and *chrysoides*) and others [9]. Actually, such cases prevail, while the "reinforcement" (discrimination of forms in the area of contact) and "character displacement" postulated by the theory have to be sought after almost with a magnifying glass [50, 53, 62], and usually the alternate explanation turns out to be more convincing.

² instead of the previous understanding of it as a sample. This change in understanding well reflects a shift from the first meaning of the word population — "number, quantity" to the second, "people". For biological species, this means the transition from analysis of a sample of individuals living in a certain area, and characterized by the average statistical values of different characteristics to the structure of relations — social, territorial, habitat and others. Relations are implemented in a particular area ("characteristic area of detection" of the group), the size of which is specifically associated with both the construction of relations in a population system, and the level and nature of the instability of the environment in which the "construction" is reproduced in the area.

- b. the indeterminacy of the species/subspecies status of well-differentiated forms from allopatric isolates of varying age created by different-scale disjunctions in the area. The classic example is the Pyrenean (2) and the Far East (6) subspecies of blue magpie *Cyanopica cyanus* (based on the phylogenetic species concept the former is distinguished as a separate species *C. cooki*) and other cases of the same kind.

Alas, the biological species concept in the form that prevailed in the 1950–1970s rather than trying to resolve these "difficult cases" was distancing itself from them, attempting to put them down to some other cases or to ignore them completely [8, 54]. Both attitudes were especially common among the supporters of the biological species concept, where by the 1980s it had finally become apparent that the isolating mechanisms are not "perfected" by selection, at least in the specially studied secondary contact hybridization zones of "well-differentiated subspecies" and other forms of birds [44] and other vertebrates [37].

A nonoperative concept that claims to be universal, in cases which, according to its own postulates, are included in its "domain" and "range of values", significantly contributed to the fact that it was shelved and superseded by competitors. Among them, in the West prevailed the phylogenetic and evolutionary concepts of species (with some others that emphasize different special cases of these two, [25, 47]), in our country it was the morphological (typological) concept [54].

On the other hand, it has discredited the very idea of the possibility of developing a universal species concept; an idea arose to replace it with a kind of **convention of species**, worked out for reasons of comprehension and usability, and then it could be possible, instead of "fruitless theoretical debates", to switch to an in-depth analysis of the interesting special cases [42].

We must admit that it is bad, bad as any routinization of a theory. The situation must be improved. What can be the essence of the improvement? First of all, it must be understood that the contradiction between the universality of the species as a category and the characteristic aspects of the notion of species in the different groups of biota (caused by the unique tradition of identification of species in each of them) is only seeming.

Once we assume after E. Mayr that "species differ not by character, but by isolation", everything falls into place. The basis of allocation of all the groups in the biota is the same *principle* (the isolation of population systems, forming a kind of "natural body" of the species, from similar systems, which form other forms of the same rank). Indeed, this principle in different groups of biota is implemented differently by taxonomers, based on different features, evidentially relating to the isolation in this particular group; the taxonomers attract amateur and personal knowledge, but to the extent that they follow just it, they identify universals, comparable on the same basis, as "species".

Another thing is that in many groups because of their poor state of exploration, high incompleteness even of the usual inventorization of forms, these principles still can not be applied, population studies of related species just haven't started or are extremely difficult. So, for example, in the studies of macrogroups of biota the cumulative curve of the number of described genera, families, and other taxa in the late twentieth century, leveled off, while the

curve of the number of species isn't even close, *except for the birds* [18, 40]. By the way, it follows that it is the ornithological material that is the most relevant for the discussion of the species concept and, more broadly, the "species problem" as such.

"Species in nature" are "Vavilov's species", population systems, effectively supporting in its specific area the integrity "inside" and the isolation from "outside". If the biological concept had closely followed his principles, it would have allocated species according to this very persistence, that is, naturally. The confronting pile of "morphological" concepts that distinguish species according to character, whether the character of the organisms themselves (species morphotype separated by the hiatus from similar morphotypes of other species) or synapomorphies that mark individual "branches" in the trees (built by phylogenetic algorithms based on various data sources), is defective if only because it does not allow either to draw or to apply such a universal principle.

4. Ways to overcome the internal contradictions of the biological concept

The biological species concept grew out of the polytypic approach to the description of species by German ornithologists Hartert and Stresemann [21]. According to it, the variation of individuals within the area was considered important, the selection of well-differentiated geographic populations with their taxonomic designation as "subspecies", etc. Hence different species are definable by one specimen, but subspecies — only in a series and, as morphological characters were "involved" in the analysis of intraspecific variation and/or isolation of intraspecific forms, the main criterion of the species turned out to be the reproductive isolation — as a "circle of races or forms" — from the others, with which it can be confused.

All isolation means **heterophobia** (term by G.A. Zavarzin [64]). It is the ability in some way to recognize 'friend' from 'foe', and reproduce only with 'friends', without "making mistakes". Or, if an error is made anyway, the ability to effectively correct it — not allowing the products of hybridization, specimens with hybrid phenotype, if they turn out viable and fertile, to become agents of implementing this error further. Which also requires recognition only at other times of the life cycle — not at the meeting of sexual partners and early courtship, but at the inclusion/non-inclusion of the individuals in the aggregation — population groups with their specific territorial / social structure (mating spots, colonies, settlements and other units). In general, with birds and mammals, solitary individuals settling outside groups, implement only the first percents of reproductive potential, with the increased risk of death [10-11].

Hence the main features of the biological species concept, as they have come to us in Russian translation by E. Mayr [34]:

- **the population-based approach instead of the typological.** The answer to the question whether the forms have reached the species level of divergence or not requires an analysis of the interaction of populations in nature (for example, the dynamics of the different phe-

notypes in the zone of secondary contact and hybridization), but not comparisons of hiatuses by the characters of museum specimens. To some extent, this is exaggeration, but without significant loss of meaning: instead of "morphology" any other indications can be used, for example, the genetic distance.

As with the analysis of any population processes and the following elementary evolutionary phenomena, we can't dispense with an analysis of selective pressures and selection processes. The latter, in general, can be both "for" and "against" the deepening of the launched hybridization.

- **species are not determined by differences, but by isolation.** The "differences" were understood as a sustained hiatus of character, "isolation" — as inability to cross with a similar form in the zone of secondary contact. "Species is a population with a closed genome" (*Table 1*), "protected" against the penetration of foreign genes and phenes through hybridization because of the ability of individuals in the area of secondary contact to "avoid mistakes" too often, so as not to produce hybrids and backcrosses. Or, if the "error" do occur, the products of hybridization show a significant reduction in the viability and/or fertility, even to complete sterility.

Therefore, an important part in the concept structure is designated to "isolating mechanisms" that ensure the latter. They are either formed during the period of separate living of forms, and in a zone of secondary contact with hybridization they only appear to stop it (if the latter does not work immediately, they are amplified by the selection to the desired level, [7, 53]). Or they don't exist until the contact and are created by selection (primarily sexual, changing the song, courtship demonstrations, etc. signs directing pair formation), "out of nothing right in the hybrid zone (*Table 1A*). Therefore, such importance is attributed to the idea of "isolating mechanisms to improve the selection", and reinforcement + character displacement as "traces" of effective "perfection".

Above, I argued the merits of the biological species concept over its opponents so hard, it's time to ask — why then, in spite of them, since 1980-90's has it been in oblivion, and the phylogenetic concept has triumphed? Why have population studies of isolation of forms in nature been substituted by the "technique" of phyloclad discernment? [1].

I think this is a direct consequence of the fact that the biological species concept, as it became popular among the masses of field naturalists in the 1960-70's underwent considerable simplification, routinization. Routinization means degradation of concept to the most obvious illustration of it, comes from the principle of economy in the form in which it can not be endorsed — the desire to save mental effort [30].

Alas, for the naturalist it is always "more fun to watch than to think", so that such bias is our professional risk. Routinisation allows fielders to explore more and more situations without wasting any time to discuss the most difficult — the domain and range of the concept. And the understanding of the biological species concept, accepted at the peak of its popularity in the 1950s and 70s, helped that a lot.

A. BCOS, TRADITIONAL UNDERSTANDING	B. PCOS	C. BCOS, OUR UNDERSTANDING
1. Theoretical content (ideology)		
<p>- The population approach instead of the typological. - Species is a population system, separate from the other population systems to the same extent to which it is integral and integrated inside</p>	<p>- Typological approach while ignoring the population in the form of "dendrogram thinking" in which any taxa are not perceived as real natural objects (groups of populations), but as a minimum units of phylogeny.</p>	<p>- The population approach instead of the typological. Species is a population system, separate from the other population systems to the same extent to which it is integral and integrated inside</p>
<p>- Species are determined not by differences but by isolation. Species actually exist in nature and are distinguished by isolation; its absence leads to considering a form to be subspecies, however much it has diverged from the original.</p>	<p>- This option is generally not included in the ontological description of the species. Species is a population, characterized by a unique combination of features and distinguished from other such forms by arbitrarily insignificant features and their combination.</p>	<p>- Species are not determined by differences and isolation. Species actually exist in nature and are distinguished by isolation; its absence leads to considering a form to be subspecies, however much it has diverged from the original.</p>
2. Suggested ways of implementation (ontology)		
<p>- Putting isolation down to inability of crossing; species is a population with a closed genome.</p> <p>- Inability of crossing arises due to low frequency of "recognition errors" during the choice of sexual partners and mating with them. Its reduction is usually associated with the failure of such matings, stopped by selection due to full or partial sterility (often in combination with reduced viability) of hybrids, but can occur at full fertility / viability of the latter. Then the selection improves the isolating mechanisms producing pre-mating obstacles to crossing de novo for the sake of saving the co-adapted gene complexes from the damaging effects of hybridization.</p>	<p>The current dominance of cladistic methods leads to a revival of the typology, as apomorphy of each clade corresponds to a feature used in the logical divisions within the construction of classifications of descending series.</p>	<p>In the area of secondary contact and hybridization — isolation of the species level specifies is dictated by the effective 'friend-foe' recognition at the moment when individuals of different phenotypes are included in the spatial-ethological structure of populations of some form; For allopatric isolates the isolation of species level is set by the comparison of the degree of divergence of the DNA-genealogies between the isolates populations with the degree of divergence of similar pedigrees of close forms with the same type of area, but having retained the intermediate populations, which have disappeared between the isolates in question.</p>

A. BCOS, TRADITIONAL UNDERSTANDING	B. PCOS	C. BCOS, OUR UNDERSTANDING
3. Application to real populations		
<ul style="list-style-type: none"> - The degree of similarity and difference between the populations is not critical. - cases of reinforcement and character displacement are essential for the proof of the status of the species - Species can be mono-, para- and polyphyletic, i.e. be comprised by many non-identical populations (polytypic species). Species is polymorphous and polytypic to the extent that is necessary for survival in fluctuating environments, it is always ready to gemmate a population, "groping" for new niches. - taxonomic "halftone" are allowed: subspecies, semispecies etc. - "Evolutionary event" and speciation are separated in time: "speciation" is the moment of acquisition by population of reproductive isolation mechanisms - Secondary contacts and hybrid zones between them act as a powerful tool for evaluating the taxonomic rank of these populations. 	<ul style="list-style-type: none"> - Species is only a monophyletic population (monotypic species). The "subspecies" category cannot exist in principle. - "Evolutionary event" and speciation happen simultaneously. - The phenomenon of secondary contact zones and hybridization is completely devoid of any heuristic value as the genetic exchange between non-identical populations is, by definition, interspecific hybridization 	<ul style="list-style-type: none"> - Population is not a sample, but a heterophobic system, the structure of which is subject to "morphological method" analysis. - The same regulatory mechanisms <i>maintain the integrity</i> of the population system of the species from the "inside" and its isolation "outside", in the secondary contacts with another form - 'Friend' recognition and 'foe' rejection is not so much on the level of marital interactions of specimens as in case of including the descendants of the former in the population structure. - Individuals very often "err", producing hybrids and backcrosses. Whether they will be the agents to enhance hybridization or not, whether the isolation of the forms continues or not is determined by their increased non-inclusion compared with "pure" specimens in the population system of both forms - Even in the course of introgressive hybridization, population systems of forms are significantly selective to an influx of foreign genes and phenes, which is why a hybrid phenotype "gets completed" only in the hybrid zone - Inflow of foreign genes into the population system, in principle, does not threaten its isolation and species status of the form, if only the "border" remains semipermeable, heterophobia is maintained, and the system successfully selects and filters the gene flow.

Table 1. Comparison of the biological species concept with the phylogenetic (currently the most popular of the "character"-based concepts). After [42], with changes.

Firstly, under the "population" of a species, *without any kind of discussion*, researchers have come to understand, "not people, but population", not a system of relationships, a specific

pattern of structure that is to be remodelled, but simply individuals who have fallen in the researcher's "box" here and now. According to R.L. Smith (1990, cited from [58], "Most of the populations have no limits, other than those made up by the ecologists themselves". Now we know that the population is structured in a species-specific manner even in a homogeneous environment, and even in it different populations indicate the presence of boundaries, connected with the internal "structure" of the system [12, 58]. Naturally, such "populations" as instant "frames" of the real structure of settlement types, different quality and detail will be incomparable between different authors working in connection with different tasks.

Second, the "isolation" of forms *again without discussion* was understood as the inability to cross at the *specimen level*: they "do not make mistakes", and do not produce hybrids, or the hybrids are fully/partly sterile. See a mention of this as common place among various authors, who have investigated the problem of the taxonomic status and hybridized and hybridogeneous forms of birds from different positions [15, 25, 44, 54]. In other words, there is a narrowing of the original meaning of the concept to the emasculation of the original theoretical content which went unnoticed, also largely for its creator. This was noted by P. Beurton in his work on the evolution of biological species concept; Mayr, in response to it, in general agreed with him [21].

The solution of another difficult problem — defining the status of allopatric isolates — was simply postponed. This supported the false belief of the opponents of the biological species concept that the latter does not have the means to breach the subject [42, 54].

Thus, it is the "internal" deformation of the biological species concept that has created its "difficulties", which it then could not resolve, though in principle they are quite solvable. First, its practical application was immediately complicated, because questions arose:

- a. What is the minimum percentatge of hybrids in the zone of secondary contact between two forms still indicates the mainenance of their isolation, and what does not, and how do we determine this threshold in a biologically meaningful way?
- b. what to do with allopatric isolates — how much should they diverge so as to be considered "isolated"? Especially considering that birds and other classes of vertebrates don't have a strict correspondence between the ranks — subspecies, species, subgenus, genus, family, etc. — and the levels of divergence, morphological or genetic. See [8, 14, 15, 44].

Second, in the routinized form, the biological species concept could not adequately interpret a whole range of empirical evidence, which is why the latter seemed to be "objections" against her. The most important of them are the following: individuals are very "often wrong", producing hybrids; and precisely in the situation of the secondary contact of similar forms the "errors" are not a rare event, they depend at least on the same factors as the "exact" recognition, which means that in certain circumstances, they can build up and thicken directionally [8, 44, 51].

Christopher Randler's survey [51] of cases of interspecific hybridization and hybrid zones among birds, testing theories of possible causes of the "recognition errors" shows that the above is a general rule. Such errors even among good species are not rare events, but a regu-

lar phenomenon (marked between 850 species, it is 10% of the world fauna). Moreover, the specific circumstances of "meeting" of the two forms on the edge of the area rather promote hybridization than hinder it. This decrease by 1-2 orders of both the number of forms in the contact area, compared with the level in similar habitats of continuous area nearby. Lack of partners of the same species here and the subsequent deprivation increases the motivation of the birds to mate with everything that somehow seems to be "legitimate" objects of courtship. More frequent depressions of numbers, leading to a particular rarity of one of the species, the "disturbances" of the environment, more common there than in the center of the area (the frequently happening "atypical" course of spring, shifting phenodates, etc.) — all this greatly increases the frequency of the "errors" individuals make, even in spite of the prezygotic isolation under normal conditions.

Therefore, individuals do not "know" that they belong to different species, and so very often interbreed with closely related forms, which is greatly facilitated by shifting of the area in space and of the number in time. This puts an end to the idea of perfecting the isolating mechanisms in an already started hybridization to prevent destruction of co-adapted gene complexes of both forms. Apparently, there are only those obstacles to the crossing which are a by-product of a separate development of forms at the stage of isolates, and the completeness of their formation only shows in the zone of secondary contact. As well as infertility in hybridization, the degree of which increases along a parabola in accordance with the model by Dobzhansky-Moeller over the time of the individual form development [35].

5. Reinforcement and character displacement in nature is a rarity, not the ordinary means of preserving the species level of isolation

The great importance of E.N.Panov's book [44] "Natural hybridization and ethological isolation in birds" — as well as the subsequent works by Y.Haffer [15] and T. Price [50] is in the demonstration of the above on a vast factual material. Although the book by E.N.Panov is not without drawbacks associated with biased expectations of the outcome³, both of the above theses, contrary to the traditional understanding of the biological species concept, were proved at least for birds.

That is independently confirmed by research in genetics of speciation, whereby hybrid zones are rather a channel for the flow of genes between closely related forms than an obstacle to it, and often the flow continues until the unification of both gene pools [56]. Further, the time of formation of the inability to cross for an "average" bird species greatly exceeds

³ The author defended the view that interspecific hybridization among birds is an important way of formation of new specific and species-like rank forms. And he included into the appendix list of conditions of hybridization everything that even remotely looked like interspecific hybridization, even cases that he could not have failed to know were not examples of it. For instance, he considered a carcass, acquired in 1929 in Europe and kept in the Berlin Museum to be a hybrid of the black-headed gull *Larus ichthyaetus* and the brown-headed gull *L.brunnicephalus*, although it is known that this was a specimen of a new kind — a relic gull *L.relictus*, discovered only in 1969 in Kazakhstan and then unknown to zoologists. Or an even more curious interpretation of the same kind — a crested shelduck *Tadorna cristata* in his list was named a hybrid (of widgeon and shelduck), although the view that it is not a separate species, but a product of hybridization, had been refuted in the early twentieth century.

the time of speciation [49]. Consequently, a large proportion of cases of differentiation at the level of forms effectively begins with the total gene pool and goes to the end (separation of the species level), without separation and divergence of the latter, rather the genetic differentiation is the result of isolation. Finally, differentiation at the level of forms appears *earlier* than at the level of genes [41, 49], and remains stable even after as a result of secondary contact with hybridization their gene pools are re-united.

"At the dawn of youth" of the biological species concept, many people thought that in response to the secondary contact and hybridization, selection in the population itself will perfect the insulating mechanisms, "protecting" the isolation from the introgression. Accordingly, a wide distribution of so-called reinforcement + character displacement was expected, when close forms are quite similar to each other in the allopatric zone, but in the contact zone and overlapping areas are the more dissimilar behaviorally, morphologically, coloration and so on, the longer the contact.

Initially the "displacement characteristics" as an adaptive process, specifically directed at the protection of isolation of the species in hybridization conditions with a similar form, was thought to include three selective processes:

1. selection against hybrids, reducing fertility and/or adaptation of the latter, "works" for the production of postzygotic isolation;
2. selection, increasing prezygotic precopulation barriers to interbreeding, improves the "mutual recognition" of species, including through the "discrepancies" of character responsible for it, thus reducing the likelihood of individuals' "errors" leading to hybridization;
3. the directed selection establishment of *de novo* initially absent isolating mechanisms that prevent malicious for both forms destructions of locally co-adapted gene complexes.

It is important that Mayr the and first generation of researchers of the 'new synthesis' considered case 3) to be crucial, since its discovery in nature would allow to consider the isolation on the species level to be a particular case of adaptation, developed essentially in the same way as other types of useful adaptations of a species to the environment.

Then, for about 50 years, all these three cases have been persistently searched for in nature, especially since it was assumed that they would be found often. Alas! They are rare, and to understand the discovered ones other schemes are more convincing than the Dobzhansky-Mayr explanation. At the same time, according to the theory, situations 1)–3) should prevail in all the "difficult cases" of incomplete speciation, secondary contact with hybridization of closely related forms, etc. Much (by 2–3 orders of magnitude) more common is a couple of cases not covered by the theory, and even directly contradicting it.

If during isolation the contact forms accumulated considerable incompatibility, hybrids are completely or partially sterile, sometimes also with reduced viability [50-51]. However, their products are in the contact zone is ongoing and the expected "plugging of leaks" is not happening — not due to the reinforcement or character displacement. Neither the reinforcement

nor the character displacement are observed in situations where the gene flow between the forms should be stopped, based on Dobzhansky's ideas.

But in cases where both reinforcement and character displacement are surely present [7, 53], an effective reduction in the intensity of hybridization in time has never been shown — for instance, for such number of generations, which is sufficient for a basic evolutionary phenomenon. These phenomena do exist, but the termination of hybridization of closely related forms, "flashing" on the frontier of one of them settling in the area of the other, is stopped in other ways, by 'friend/foe' recognition of the population systems of both.

In other words, now we can openly say that the expectations of the classics were not confirmed, and the isolation of the species level is maintained otherwise. It is important that it is the problems with the search for "perfection of isolating mechanisms" in nature contributed to the loss of interest in the biological species concept in the early 1980s. That is, the decline of interest began even before the rise of phylogeography, "dendrogram thinking" and the phylogenetic species concept, which are usually stated as reasons for it [1].

Situations 1) and 2) provided by Dobzhansky's model, happen in nature, but much more seldom than the theory. In addition, the vast majority of examples of reinforcement, presented in the surveys [7, 53] etc., are much better explained not by Dobzhansky's model, but by two other methods.

The first is: the observed reinforcement nor the character displacement in the contact zone is the consequence and the effect of trends of variation connected to the adaptation of each form to the environmental conditions of its main area (for example, climatic gradients, changes in vegetation structure in the populated habitats, etc.).

This is just because these trends are opposite to each other, among other things, because the "splitting off" of child forms of the original is often associated with the adaptation to the territories with conditions alternative to those in the historical center of the area. Since both forms before the secondary contact spread from the refuges towards each other, it is clear that associated with them difference in morphology, behavior, etc., to be found there will be the greatest. Therefore, the reinforcement is often asymmetrical, is seen only in one of the forms or is stronger in one form than the other.

The second alternative explanation is as follows. The observer, looking for confirmation of the idea of "perfection of isolating mechanisms", sees it in something that in fact is a fixation of the beginning of population systems "splitting" due to the mechanism we proposed for the 'friend/foe' recognition. This impression is created due to the presence of reinforcement or the character displacement and defectiveness of hybrids between two forms. In this case, hybridization does not ever stop, the "leak" is not plugged, and yet the "cost of eliminating" inferior hybrids is "bearable" for both forms, the "reproductive self-destruction" doesn't happen. A good example here is the relationship of benthic and limnetic forms of three-spined stickleback *Gasterosteus aculeatus* in the post-glacial lakes of North America, described in [53], as well as the above mentioned "splitting" of population systems among birds.

50 years of research into speciation in nature showed that the divergence of forms (including when it is distinct populations within the maternal species) and the formation of isolation at

the species level — are processes that take place in different moments, "protected" by different mechanisms, etc. Accordingly, the required reinforcement in practice is rare and almost always can be explained otherwise. But the "perfection of isolating mechanisms" does not happen at all.

In other words, a survey of modern data on this issue confirms the old idea of Darwin (1939, cited from [44]) that the forms' inability to cross (as well as infertility in hybridization) is not a selective advantage and is not accumulated by selection directly. The latter occurs indirectly, through a period of isolation of the separated forms [53, 56]. Consequently, the separation of species is a non-linear function of the time they stay in isolation.

Much better than with the idea of character reinforcement, all of the above is consistent

- a. with the Dobzhansky — Moeller model of formation of hybrid incompatibility
- b. with our model maintaining the isolation at the species level, according to which the main obstacle to the crossing is not created in the time of formation of the mixed pairs and the production of hybrids, but at the "integration" of hybrids and backcrosses in the population groups of each form [9].

Mechanisms postulated by b) assist the mechanisms postulated by a) and vice versa. According to the Dobzhansky — Moeller model, the gradual accumulation of innovations in the genes of the "friend" form produces the side effect of quadratically increasing reproductive incompatibility with "foe" forms of the same kind, because selection can not "test" their compatibility with innovations that accumulate in homologous genes of the "foe" gene pool. Therefore b) will necessarily lead to the fact that despite the formal presence of intense hybridization, "clean" specimens of both forms live and breed mainly in the environment of other "clean" ones, which actually form the groups.

While hybrids, even numerically dominant in the hybrid zone, *do not form* their own groups, but *one by one* join the settlements of some form or reproduce outside the settlements — with predictably poor results. Thanks to that, the possibility to test new fixed mutations for "compatibility" with the innovations in the gene pool of another form drops dramatically before *any meaningful cesure of hybridization*, genetic incompatibility of forms increases, which, with the continued production of hybrids and backcrosses, reduces the stability of their behavior and the ability to create their own stable groups, even with the numerical dominance. The circle closes.

If b) is true, then there is a synergy between the behavioral (or ecological) mechanisms to maintain isolation and the genetic incompatibility between the two forms due to which cases of contact either "merge" population systems into one, or allow preservation of an isolation for an unlimited time, "confirming" the achievement of the species level. But if "the traditional form" of the biological species concept is true (where the main point of 'friend/foe' recognition depends on whether mixed couples are formed or not), such synergy will not be observed. If so, the two sides of the overall process of speciation — precopulation and postzygotic isolation mechanisms (*species recognition* and *hybrids incompatibility*) are mutually exclusive, and not connected by positive correlation.

This result is quite verifiable. Indeed, among birds are observed

- either (for the youngest species) isolation, created by b) type mechanisms and sustainable differentiation of forms in the absence of genetic incompatibility, and often with a completely common gene pool, "mixed" by introgressive hybridization,
- or (for the "good species") a positive correlation between the degree of *species recognition* and *hybrids incompatibility* in some forms (the former reflects the development of the pre-copulation, the latter — postcopulation barriers to crossing) [7, 43, 49]. The traditional view of the speciation involves the *regression of the process* — first the accumulation of genetic changes that lead to inconsistencies, in the period of independent development, then during the secondary contact with hybridization — a rapid development of behavioral and morphological adaptations such as "mating plumage" within the framework of perfection of isolating mechanisms [7, 52].

In reality, with the birds and other vertebrates, we are seeing the opposite — differentiation of forms at the species level often begins and ends before gaining the inability to cross, it is possible with a fully common gene pool. Conversely, the effective separation of population systems of two forms by the b) mechanism accelerates the slow and gradual development of the inability to cross, lagging far behind the pace of speciation [41, 49].

In cases of real character reinforcement, selection against hybrids or selection towards better recognition in the formation of pairs, which increases the contacting forms isolation from each other, produces, as a rule, an external biocenotic agent. It can be insect pollinators with their different reaction to the flowers of different colors, different species-models to simulate, which the developing forms of mimicing species begin to imitate, carnivorous bats, catching tree frogs, focusing on the mating male calls, etc. See [35, 53].

In a general case there might not be a biocenotic agent, and most likely there won't be one; most predators, pollinators, etc. are not so specialized to detect the differences in the signals of the incipient species. At the same time, the process of speciation in all species concepts, including the original understanding of Darwin [37] is thought of as proceeding spontaneously, affected only by the internal forces.

6. The "Renaissance" of the biological species concept: Possible approaches

Appealing to the data on hybridization as to objections, the proponents of alternative concepts (especially typological, phylogenetic and evolutionary) by the early 2000's actually excluded the biological concept from the list of discussed, especially in the West [1-2, 65].

However, the obvious disadvantages of alternative concepts are demanding the restoration of the latter on more grounds than ever, which allows to incorporate the objections and use them for the development of the concept. It is possible to put forward the following theses for its recovery, returning to the original understanding of the two key

points related to population-based approach and isolation as a criterion of species-level differentiation of forms.

- Population is not a sample, but a heterophobic system, the structure of which is to be analysed by the "morphological method".
- The same regulatory mechanisms *maintain the integrity* of the population system of the species "inside" and *its isolation from "outside"*, during the secondary contact with another form
- The viability of populations "sitting" on a "center-periphery" gradient of the species area is much more defined by the inflow of non-residents than by the local reproduction and local adaptations.
- Resettlement of individuals leads to differentiation of populations, and not to "blurring the differences", because individuals are sorted according to behavioral potentiality.
- 'Friend' recognition and 'foe' rejection is not so much on the level of mating interactions of individuals as when the descendants of the former are integrated in the population structure.
- Individuals very often "err", producing hybrids and backcrosses. Whether they become agents of hybridization enhancement or not, whether the isolation of the forms is continued or not, is determined by the worst position on which they are included in comparison with "pure" individuals in the population system of both forms
- Even with introgressive hybridization, population systems of forms are substantially selective to an influx of foreign genes and phenes, which is why a hybrid phenotype is "put together" only in the hybrid zone
- Like the presence of a foreign currency in the pocket does not make us closer to the psychological makeup of its residents, so the inflow of foreign genes in the population system, in principle, does not threaten its isolation and the species status of the form. If only the "border" is semipermeable, heterophobia is maintained, and the system successfully selects and filters the gene flow, that is, it is taken under control. Overall, current evidence supports the conclusion by E.N.Panov [44] on the creative role of hybridization processes in the zones of secondary contact of the "separated" initially allopatric species. But they did not "create" new hybridogeneous forms that can exist along with the parent ones, but provides the parent forms with the "necessary" genes and phenes to adapt either to a hybrid zone habitats or other conditions of the area, without disturbing the original isolation of both.

Thus, according to mtDNA, common mallards and spotbills are "like crows" [28], gene pools have joined together, but the forms remain isolated. This situation is different from hybridization with American black duck *Anas rubripes* in the U.S., where there is a classical Mayr's "merging of forms" [34]. The same situation as for common mallards and spotbills is viewed for six sympatric species of ducks, as the mallard, gadwall, pintail, wigeon, teal and tufted duck, despite the fact that the last three species are far enough from the first three. Gene ex-

change through hybridization (preserving fertility and viability of hybrids) between these species has been so great that the authors compare it with the "horizontal transfer" of genes in bacteria. However, the "blurring" of species boundaries hasn't happened even here [24].

An interesting point is that, unlike the mallard, forms such as *Anas zonorhyncha* and *Anas rubripes* are "female-coloured" and don't have bright males significantly different from females in coloration, "braids" of decorating feathers, etc. Furthermore, in all experiments, where females of "female-coloured" forms had to choose different males, the colorful, heavy and strong mallard drake is invariably beyond competition. Females prefer him, rejecting the "humble" males of their own species. Therefore, it was believed that in nature the hybridization is always asymmetrical: male mallards breed with females of monomorphic species. However, nature reveals no less powerful gene flow associated with the hybridization in the opposite direction, which is easily detected by mtDNA analysis, when the hybrid population is dominated by haplotypes not of monomorphic species, but of mallard [28]. Apparently, this is a consequence of interactions related to the "dark side" like forced copulation after pairing.

In summary, the proposed improvement of the biological species concept can be illustrated by the addition of the third column of *Table 1*, opposing the biological species concept (in the traditional sense) to the phylogenetic.

Indeed, the main idea that is firmly confirmed from the original concept — is the discreteness of species, and the reality of their existence in the wild. Including the situations of secondary contact of forms. Hybrid zone is either restricted by narrow limits and constant over time despite the long-standing hybridization (but is not reduced, because there is no "perfection of the isolating mechanisms"). Or, if the form does not reach the level of species, introgression between them in the hybrid zone deepens, the latter "blurs". Eventually, a new hybridogeneous population emerges, joining the previously independent forms A and B into a single population system, in fact another subspecies among subspecies, with restoration of variability trends to a smooth cline. Such, for instance, is the situation in the zone of contact of European and Siberian chiffchaff *Phylloscopus collybita abietinus* and *Ph.c.tristis* in the Cis-Ural region and in the Urals. As a result of the unobstructed deepening of hybridization, the contact zone "blurred" over a vast territory occupied by hybridogeneous form *fulvescens*, in fact, yet another in a series of other subspecies. This "natural experiment" shows that both chiffchaffs, no matter how much they separated, still fall short of the level of species: their secondary contact restored the unity of the population system [31].

Here we propose the idea of "own-alien" recognition following the inclusion of phenotypic variant individuals into the spatial and ethological structure of both populations, differing in their phenofoms. This mechanism could explain the phenomenon of populations isolation without obvious hybridization obstacles. In case of close similarity of biological forms hybrid offsprings are to be characterized with normal survival and reproduction abilities. In the other case these properties of hybrids should be significantly reduced. Therefore in the latter variant there is no hybridogenic population forming. By the way, isolated crossbreeding cases occur more of less frequently. In that follows, some hybridization obstacles proba-

bly could arise and stop crossbreeding. On the contrary, without such preventing mechanisms, hybridization frequency remains stable.

There is an prominent example of rapid settlement of Syrian woodpecker *Dendrocopos syriacus* in the “traditional” into the natural habitat of great spotted woodpecker *D.major*. The first species was previously resident of Balkans and Asia Minor. Since 1930s it moved to north and east: in 1994 it was found the Uzhgorod; during next 50 years it was spread in Ukraine; in 90s it reached Voronezh and Volgograd regions and further “ended the circle” in Ciscaucasia. During first years of this travel the ourbursts of crossbreeding were detected (I have also seen several mixed pairs), while later the hybridization reduced [6]. There were a lot of causes of such effect: the allobiotope establishments due to Syrian woodpecker preference to gardens and parks during dissemination; the destabilization of hybrids behavior including those with normal reproductive possibilities. Such birds were characterized with disorders in the search of potential partner. In individual cases the reaction of hybrids to specific stimuli varied a lot including even more strong response than for “pure” ones. However, such response was both less stable and less specific. Consequently, the offsprings of mixed pairs were in disadvantage to pure ones during partner searching and/or territories occupation especially in the higher probability of occasional migration [6, 8].

Another interesting observation was described for two chipmunk species from the Rockies: *Tamias ruficaudus* and *T.amoenus*. These chipminks vary significantly basing on their baculum morphology. Previously baculum differences were considered as a guarantee from hybridization. Surprisingly, the frequent traces of alien mtDNA introgression were revealed for these non-sister species. Three described evolutionary events probably were associated with recent asymmetric mtDNA introgression in morphologically distinct secondary contact zones. Additionally, the traces of ancient hybridization events leading to alien mtDNA fixation were also detected. By the way, such events were characterized with the unchanged phenotype and remaining “own” nuclear DNA [13].

In is well-known that in the case of inter-species hybridization of birds most of mixed pairs are unstable with the duration of “staying together” varying from hours to several days. It is true for forms differing in their signaling repertoires. But the remaining mixed pairs could be extremely stable for the whole season and even during several years. The fraction of such stable “misalliances” is higher if signaling languages are more similar. Note that this effect is independent on the descendants survival and even on the fertilization of eggs [8, 44]. For example, in the narrow contact zone of two shrikes, *Lanius collurio* and *L.cristatus* in the Western Siberia, mixed pairs were described. Most of such “marriages” are quickly ended due to different signaling repertoires. But the rare cases of stable mixed *Lanius* pairs are characterized with viable and fertile offsprings [26].

In such cases *one-type* signals provide recognition of aliens and fast decay of a part of “misalliances” after initial contacts of excited individuals. The *other-type* signals (or another signaling regime) support the “survived” pairs stability. As expected, these “other” signals just minimally diverge between closely related taxa. For example, for two South African turtle-dove species, the *Streptopelia vinacea* and *S.capensis*, the narrow hybridization zone in Uganda was described. This region population contains the stable fraction of viable and fertile

hybrids. Both birds are capable of producing homologous signals: “cooing at roost” and “cooing in bow”. The stereotypic usage of these signals is important for the protection of the territory and/or for attracting potential partners there. However, the reproductive behavior and corresponding signals vary for these birds.

Consequently, the first “territorial” signals, but not the second “reproductive” signals lead to preferential choice of “owns”, not “aliens” in the allopatric areas – but not in the hybrid zone [17, 22-23]. Respectively, the first shout type provide heterophobia of both populations and the second one consolidates pairs formed after “filtering” at the first step. Hybrids are characterized with disordered “mixed” in varying proportions signals, as it was shown basing on the acoustic comparative analysis. Unlike parents, the hybrids are unable to distinguish “owns” and “aliens”: their response to the “cooing on the roost” is independent from the similarity of this signal acoustic characteristics to their own. Saying more, their response is *worse* in comparison to “pure” individuals and “own” signals. Consequently, hybrids are defective in territorial seizure and potential female partners attraction [17, 22-23]. While speaking on the parental species, let us note that the response to the “cooing on the roost” of *S.vinaceae* is stronger than to those of *S.capensis* in allopatric populations. This asymmetry persists in hybrid offspring, thus the hybridization is also asymmetric: the *capensis* area is enlarging into the *vinacea* area, but not vice versa. Despite the remaining isolation of these forms, the *vinacea* alleles are frequently added into the gene pool of *capensis*. Nevertheless, outside the hybridization zone both morphology and behavior of *capensis* is unchanged from the normal features of this species [17, 22-23].

Traditionally the classics (and Mayr, especially) proposed the populational approach, not the typological. But this idea contained the time bomb exploded in 70-80s: there are some forms. Are they differentiated enough to be considered as species? It’s impossible to answer this question without typological approach [29]. However the typological procedures should be *discussed and taken under control* initially and not passed over silence: thus, the populationism could use them. The “natural typology” of systems of populations may be developed based on the described above morphological approach to their structure and dynamics. This way allows us to reconstruct the “natural formation” with it’s inner regulators providing the ethological and populational structure despite the environmental instability outside and the stochastic demography inside the system [10]. The reason is that any ideology lacks the indispensable components and methods, they in any case “pierce their way” – but probably in a spontaneous barbaric manner.

Indeed, the application of *such* a typology for the analysis of intraspecific variation and interspecific hiatuses could be helpful for solving the following old problem of biological concepts of species: the time-stable hybrid zones of two forms. Such zones remains narrow without tendencies to grow in spite of the long-standing period of hybridization (hundreds and thousands of years) and the overall viability and fertility of hybrid offspring (leading to common gene pools for contacting species).

The number of such forms could be different and greater than two. The common area of the “race circle” contains numerous their subtypes, located serially just like beads on a string and hybridizing in pairs and/or totally. The example of such “race circle” is known for gold-

en woodpecker *Colaptes auratus s.l. – auratus s.str., cafer* and *chrysoides* in North America [38-39, 60]. Another case was revealed for black wheatear *Oenanthe picata – picata, capistrata* and *opistoleuca* [45]. By the way, the classic case of stable narrow hybridization zones between black and gray crows could be included here also.

Here we have presented just a few examples among numerous ones [see reviews: 43]. All of them illustrate the possibility of common gene pool emergence and phenotypes mixing as a result of long-term crossbreeding. The molecular genetic evidences of this phenomenon were published, for example, for black and gray crows [16, 27]. Several markers between neighboring crow groups in the hybridization zone demonstrate the similar level of differences as those for black crows of Eastern and Western Siberia or for gray and black crows. Furthermore, the form B phenes are spread far to the habitat of the form A up to the third form intergradation [see fig. 81 in 45].

What one can see in such a situation? The commonality of gene pools and long history of hybridization makes in theoretically possible that in the *area of the form A* the significant fraction (up to 5-15%) of *hybrid A-B phenotype* could exist. Such phenotype may consist of numerous XYZ features characterized by opposite values in A and B forms and combined – in hybrids. However, this mixed phenotype occurs only in *hybrid zone*! On the contrary, such “alien” phenes in form A and B areas could be found only one by one and not in complex. These findings are the more interesting the more prominent phenotypically distinct features could be found for hybrids. Such phenofoms were even described as species [44].

Let us look at the example: the above mentioned golden woodpeckers are characterized with the hybrid phenotype A-B, which additionally to A/B contact zone arises in the hybridization boundary with form C (as well as the hybrid A-C phenotype) [38-39, 60]. This remarkable fact tells us that the B-form signs successfully crossed the total form A habitat; but the hybrid A-B phenotype couldn't be generated (in contrast to “pure” B forms) in other place than the hybridization zone – even *other* than A-B. In the inner form A area these phenes could be found only separately, not together. However, the argued molecular genetic basics without enhancement of isolation mechanisms are insufficient for explaining listed observations.

Are there any missed factors of natural selection? We propose the impact of ontogenesis here. The population structure in the “inner” habitat of species is strongly regulated and stabilized using various mechanisms. For example, the “incorrect” behavior of individual leads to it's “culling”. The normal course of ontogenesis under such conditions excludes the “alien” phenes. In extreme cases, they could be expressed only as separate signs. Thus, the final morphotype is formed under the pronounced regulatory pressure selecting mostly “own” but not “alien” phenes [9].

The narrow zone at the area borders of contacting species does not allow such “morphoselective” mechanisms to work and to switch on the recognition of “owns” and “aliens”. Therefore, the hybrid morphotypes occur only in such crossbreeding loci. The population “soup” already contains all gene- and phene components, and the only thing you need to collect the hybrid puzzle is the shutdown of listed regulators. At the narrow strip of hybrid-

zation zone the structure of relations, behavioral traits and other features are disordered and the overall population is destabilized.

It's no wonder that population sizes in *the same loci* of hybrid zone are up to two orders smaller than in the *nearest* allopatric loci. Therefore such "demographic" decrease is unrelated to such expected factors: extreme environmental conditions, bad quality of habitats etc. The real reason is the lack of stable networks of groups and migrating individuals between them: population structure should be formed only through cooperation and integration. The boundaries of species areas lack such systemic interconnections or, probably, they are extremely destabilized [10-11]. It is important to note that the abilities to distinguish and sort "owns" and "aliens" are better at the level of population system, not at the individual level. These effects are prominent both for case of population-forming behavior and relations and in the case of morphotype-forming ontogenesis.

Therefore, both contacting species are able to persist as somehow isolated forms in spite of their long-term history of introgressive hybridization [4, 5]. Such a phenomenon include various features: morphological, behavioral, environmental, biotopic specialization etc. Indeed, recent studies of gene flux through hybridization zone demonstrate that both forms are *highly selective* to the choice of particular genomic elements to be introduced into the hybrid gene pools [reviewed in 56].

Mitochondrial DNA is prone to integration into other species genome. Thus, those groups where males were heterogametic, could be considered using Haldane rule: mtDNA is female-inherited and, additionally, females are highly fertile. Surprisingly, the similar effects were described for BIRDS – known to be female-heterogametic. In several cases it was shown that the "alien" mtDNA have replaced "own" mtDNA totally (for *Vermivora pinus* and *V. chrysoptera*). However, the "alien" mtDNA pervasion is significantly asymmetric illustrating the existence of selection "filters" for gene exchange. The pronounced asymmetry of mtDNA invasion was revealed in 50 among 80 cases [63].

As for nuclear DNA, it's recombinational hotspots are known to be mostly introduced into alien genomes. These loci are short and their shortness is also associated with high recombination frequency. The Dobzhansky-Muller hypothesis fits well these data: the genomic incompatibility between species is considered to be associated with a few genes, prone to recombination and providing better adaptation of their carriers. Other loci, even fast evolving but slowly recombining – such as pericentromeric heterochromatin – are rarely adopted [56]. Moreover, pericentromeric regions are connected with building the barrier for interspecies hybridization.

Such mechanisms probably regulate individual development of forms under the pressure of scud of the invasive alien genes. All these pathways lead to preferences of "pure" morphoforms in each area and complicate the development of mixed phenotypes in other places than contacting area [9].

Thus in the common area of both forms "alien" phenes could be realized only partially, as a traces in addition to "normal" phenotypes: even in the case of significant fraction of genetic hybrids and enhanced introgression.

In the recent review [56] it was noted that hybrid zones were not *barriers* but *channels* for gene exchange. Various factors of natural selection don't stop the introgression – just make it asymmetric. The examples were shown for *Cyanoliseus patagonus* [33], *Manacus vitellinus* [61], *Foudia* [62] and other species. In case of reaching the higher level of isolation these form can form new species through the forming of regulatory mechanisms for such gene exchange. The “maturity” of such regulatory mechanism(s) gives us an indication of the real *species* differentiation level (including numerous populational, morphological, molecular-genetic and other characteristics).

Genetic processes only couldn't lead to proper isolation without further selective pathways: lacking these selectors all specific morphotypes should be connected in the continuum. But mostly we reveal the opposite effects confirming therefore the presence of evolutionary selective mechanism preferring distinct morphotypes. This mechanism doesn't deal with such features as crossbreeding barriers, ethological signals, behavioral species recognition, hybrids incompatibility etc. My idea is that THIS mechanism works well only at *population* level, not individuals. And thus the offspring of proper or mistaken breeding are integrated into the whole population structure.

The secondary contact zone with frequent crossbreeding is characterized with stable colonies of A and B forms separately. While the hybrids and back-crosses are able only to accompany pure “citizens” and can't form the populational units. That's why the “improper” individuals inclusion into population and their reproduction probability is low. Thus, the individual-level breeding mistakes are corrected at this population level. Hybrids and back-crosses are fertile enough but they are “deprived of their rights” to deepen the reproductive influence. Different hybrid variants are sorted between A-form and B-form habitats exposing to stabilizing selection (with various selective morphological, biotopic and behavioral parameters). The “improper” phenotypically hybrid individuals are unable to integrate to normal population “etiquette” – during their lifespan and/or reproduction. The behavioural standard should be involved significantly in such culling mechanisms: the mixed signaling of hybrids leads to frequent mistakes in contrast to “pure” ones [9].

The heterophobic events at the boundary of two populations could be demonstrated using the well-known sponges experiment. They were grinded extremely to single cells and then mixed. The components of this “cocktail” reassociate with their specific cellular partners, not aliens. Therefore, the key stage of breaking or stabilization of the isolating barrier between populations is the *inclusion* of the offspring into the population structure, but not their fertility or other features. The mechanism of such “culling” is the *communication*. The proper generation of this mechanism stabilize the populations and their isolation even in the presence of frequent crossbreeding with fertile hybrid offspring. It seems that our ideas work well also for variable systems with subspecies or races characterized with differences in sizes, melanization, coloring etc. Therefore there could be distinct *unbiased* signs of *species*, not of *subspecies*. The absence of “culling” mechanism in studied populations let us consider them as single species despite any measured morphological variations.

7. The problem of allopatry

The most complicated case of our analysis is the situation with allopatric isolates. How one can determine when the level of biological divergence is high enough to consider the isolates as distinct species? Noteworthy, the baseline of divergence is always present for such objects, including cases of “well-differentiated subspecies”.

The answer is simple, indeed. Using the proposed morphological approach to populations analysis we can describe:

- the *species* = the Vavilov’s species definition as a system of populations interacting inside the area and differentiating at the boundaries at the center- periphery gradient basing on the flux of migrating individuals;
- the *species* remains intact until it’s interior populations are integrated through the stable exchange of individuals. Such traffic don’t smear the differences between subpopulations, on the contrary, it enchances the differentiation due to selection of “proper” individuals [10-11]. In the case of stable reduction of the population size and/or ecological changes leading to area fragmentation the several, mostly peripheric loci, are prone to further differentiation even up to the level of new species. How can we detect it if the area is already fragmented and the secondary hybridization is impossible?
- Before the separation of “far populations” to the isolate(s) the species area is gradiented in the center-periphery direction. Most event of differentiation are distributed along this axis. The social stress and the competition are more important in the center characterized with dense population. As for environmental stress, it’s pressure is stronger at the periphery. Thus, individuals are sorted geographically according their abilities to overcome the first – or the second stresses (Fig.1).

This mechanism provide further differentiation between contacting populations not *despite*, but *through* the stable migration amongst, and the variants of patientness-competitiveness of life strategies could be distributed in a bell-shaped curve for both populations (Fig.1).

The specific systemic pattern the the key *regulator* and “*controlling force*”, and the individuals migration, communication etc. form the *controlled* response. I propose that the whole morphoecological differentiation between isolates was present at the stages of their presence inside the integral population system of the same species. The period of isolated provide the grow of separation only.

Thus, the metrics of the specific differences for allopatric isolates could be easily proposed (for example, for the case of blue magpies from Pyrenees and the Far East. The molecular-genetic divergence values between them should be compared to those between related species with the similar area(s) which are still connected.

The *Pica pica* magpie with it’s European and Far East races is perfectly suited for this purpose; also one can study such Corvidae species as *Cyanopica cyana* and it’s Far East *pastinator* form as well as *Corvus monedula* and *C.monedula dauricus* [16, 25, 27]. Transpaleoartic Corvi-

dae species studied by Kryukov's group could be considered as a good data for the case of conclude the state of blue magpies (basing on the *C.corax*, *Perisoreus infaustus*, *Nucifraga caryocatactes* etc). Other allopatric situations could be analyzed by similar way.

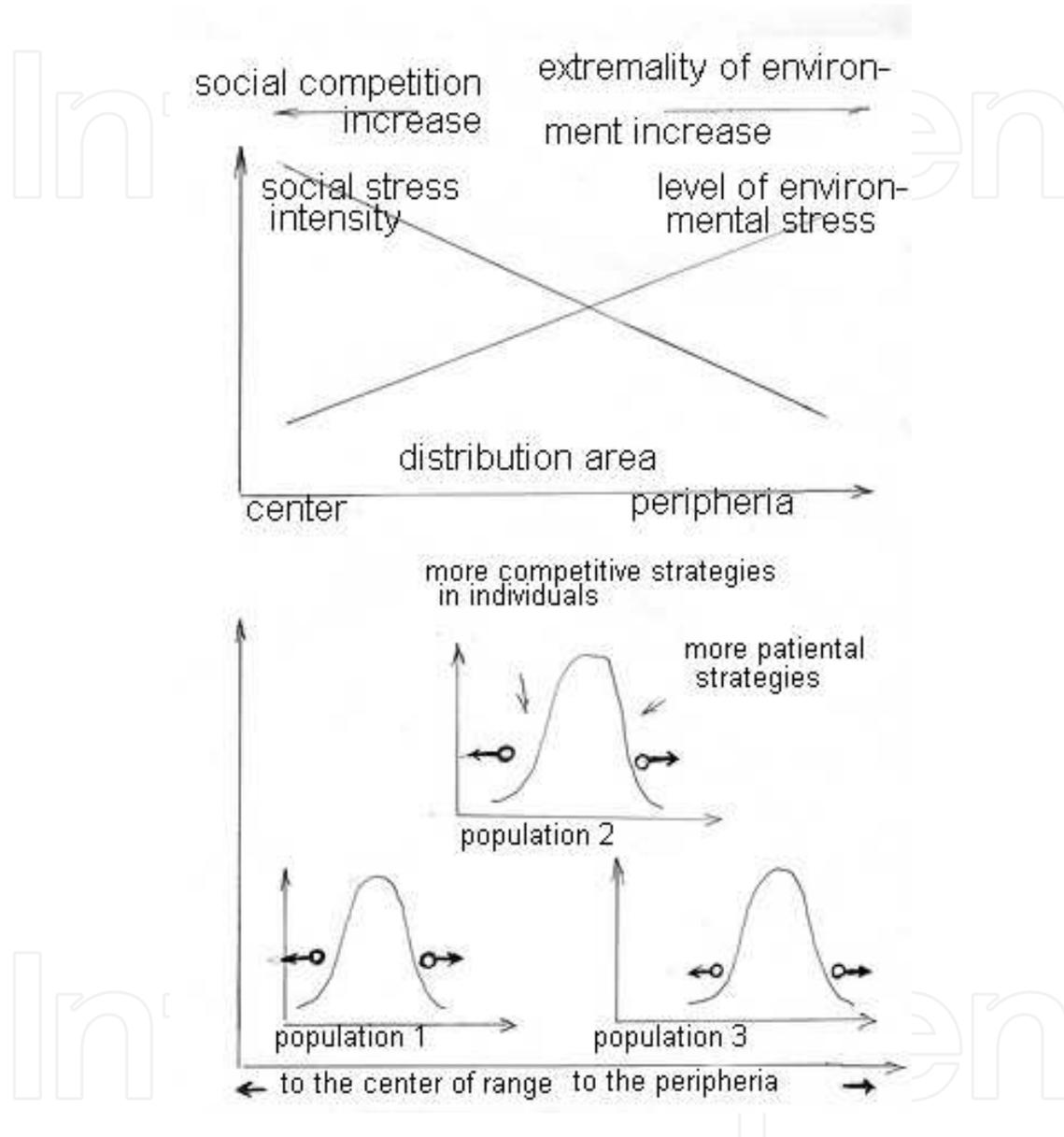


Figure 1. Population system of the form according to the "morphological approach". gradients "center - periphery" of the range (top), sorted by species potencies (degree of competition and patience strategies) along these lines (bottom).

Finally, these data demonstrates that various *Corvidae* are able to form divergent Eastern and Western subtypes with varying level of differences. This level is high and equal for magpies and blue magpies but higher in comparison to rooks or jackdaws. Thus, the blue magpies are not unique and these populations are still the same species: the difference between Eastern and Western populations is quite similar to those for other magpie population system characterized by continuous area.

8. Conclusion

The biological species concept is defined *biologically* according to our aim to divide the total biodiversity into *real* classes. The supra-individual systems – populations and species – are characterized by the presence of regulators stabilizing their integrity and isolation from other similar systems. Various mechanisms are involved in the process: gene pool(s), migration, communication, ontogenesis etc [see 3]. This “natural control pathway” works like the restorer of ancient paintings.

Let us overcome the last complication: the species are present in all taxa. But only the well-studied phyla give us enough data to distinguish species correctly. For others we know only several individuals and nothing about their populations.

Thus, the species should be defined basing on the presence of the precise hiatus, using morphological conception and typological approach. It is convenient but depends on the stability of the hiatus – and this stability is unknown.

If new data destroy the previously defined classification we're to start the work again. We'd prefer to use more “natural” classifiers stable to such new findings. But there are still two poles basing on the prevalent role of the typological (morphological species concept) or populationist approaches (biological species concept). All other concepts are based also on the same features while the influences of these two approaches are combined in different proportions.

The species problem is associated with difficulties in reaching the proper compromise here – and remaining the usability of the proposed classifiers.

Acknowledgements

I am grateful to Igor Yakovlevitch Pavlinov for the invitation to talk about species problem in Zoological Museum; it helped me to bring order to my thinking and this article preparation. I am also thankful to A.A.Makhrov, S.V.Polevova and A.A.Pozdnyakov for their remarks and discussions. I'd like to thank VIGG researchers M.V.Friedmann and N.Yu.Oparina for their help and consultations on the genetic mechanisms of hybridization barriers and other discussions.

Author details

V. S. Friedmann

Moscow State University, Faculty of Biology, Moscow, Russia

References

- [1] Abramson N.I. Molecular markers, phylogeography and search for the criteria for delimiting species// Trudy ZIN. 2009; 313 (1) Suppl. 185-198. [in Russian, English summary].
- [2] Altukhov Yu.P. Genetic processes in populations. Moscow: Akademkniga; 2003. [in Russian, English summary].
- [3] Artamonova V.S., Makhrov A.A. Genetical systems as regulators for adaptation and speciation processes (toward the system theory of microevolution)// Modern problems of biological evolution. Proceedings of the Int. Conference on the 100th anniversary of the State Darwin Museum. 2008. 381-401. [in Russian].
- [4] Bell D.A. Genetic differentiation, geographic variation and hybridization in gulls of the *Larus glaucescens-occidentalis* complex // Condor. 1996; 98(3) 527-546.
- [5] Bell D.A. Hybridization and reproductive performance in gulls of the *Larus glaucescens-occidentalis* complex// Condor. 1997; 99 585-594.
- [6] Butyev V.T., Friedmann V.S. Great spotted woodpecker. Syrian Woodpecker. Middle spotted woodpecker. White-backed woodpecker. Three-toed woodpecker // Birds of Russia and neighboring regions. From Owls to Woodpeckers. Moscow: KMK Scientific Press; 2005. 325-398. [in Russian, English summary].
- [7] Edwards S.V., Kingan S.B., Calkins J.D., Balakrishnan Ch.N., Jennings W.B. Swanson W.J., Sorenson M.D. Speciation in birds: Genes, geography, and sexual selection// PNAS. 2007; 102 6550-6557.
- [8] Friedmann V.S. The communication in the mixed pairs between different species of woodpeckers: some ethological barriers to mating // Zh. Obshchei biologii. 1993; 54 (1) 294-310. [in Russian, English summary].
- [9] Friedmann V.S. 'Friend-foe' recognition systems and the Renaissance of the biological species concept// Modern problems of evolution. XXIth reading by A.Lyubishchev. Ulyanovsk; 2007 201-215. <http://www.evolbiol.ru/fridman.doc> [in Russian, English summary].
- [10] Friedmann V.S. Communication signals in vertebrates: from stimulus to symbols. Part 2., chapter 2.5. Population as a complex system and communication tasks. M.: URSS; 2012 160-190. [in Russian, English summary].
- [11] Friedmann V.S., Eremkin G.S. Urbanization in "wild" bird species in context of urban landscape evolution. Moscow: URSS; 2009.
- [12] Goltsman D.W. Differentiation by dispersal // Nature. 2005; 433 (6) 23-24.
- [13] Good J.M., Demboski J.R., Nagorsen D.W., Sullivan J. Phylogeography and introgressive hybridization: chipmunks (Genus *Tamias*) in the northern Rocky Mountains // Evolution (USA). 2003; 57 (8) 1900-1916.

- [14] Grant P.B., Grant R.B. Speciation and Hybridization in Island Birds [and Discussion] // *Phil. Trans. R. Soc. Lond. B* 1996; 351 765-772.
- [15] Haffer J. Parapatrische Vogelarten der paläarktischen Region// *Journal of Ornithology*. 1989; 130 (4) 475-512.
- [16] Haring E., Gamauf A., Kryukov A. Phylogeographic patterns in widespread corvid birds // *Molecular Phylogenetics and Evolution*. 2007; 45 840-862.
- [17] den Hartog P.M., de Kort S.R., ten Cate C. Hybrid vocalizations are effective within, but not outside, an avian hybrid zone// *Behav. Ecol. Vol.* 2007; 18 608-614.
- [18] Joppa L.N., Roberts D.L., Pimm S.L. The population ecology and social behaviour of taxonomists // *Trends of Ecology and Evolution*. 2011; 26 (11) 551-553.
- [19] Kerimov A.B., Ivankina E.V. The proportion of current and final indicators of reproductive success of individuals in the suburban population of the Great Tit, *Parus major* L. // *Trudy Zvenigorodskoi biologicheskoi stantsii*. 2005; 4 221-231. [in Russian, English summary].
- [20] Kharitonov S.P. Waterbird colony structure: system approach. // *Ornithology*. Moscow; MSU Publ. 1998; 27 C.26-37. [in Russian, English summary].
- [21] Kolchinski E.I. Ernst Mayr and modern evolutionary synthesis. Moscow: KMK Publ.; 2006. [in Russian].
- [22] de Kort S.R., den Hartog P.M., ten Cate C. Vocal Signals, Isolation and Hybridization in the Vinaceous Dove (*Streptopelia vinacea*) and the Ring-Necked Dove (*S. capicola*)// *Behavioral Ecology and Sociobiology*. 2002a; 51 (4) 378-385
- [23] de Kort S.R., den Hartog P.M., ten Cate C. Diverge or merge? The effect of sympatric occurrence on the territorial vocalizations of the vinaceous dove *Streptopelia vinacea* and the ring-necked dove *S. capicola* // *J. of Avian Biology*. 2002b; 33 150-158.
- [24] Kraus R.H.S., Kerstens H.H.D., van Hooft P., Megens H.-J., Elmberg J., et al. Widespread horizontal genomic exchange does not erode species barriers among sympatric ducks// *BMC Evolutionary Biology*. 2012; 12 45 <http://www.biomedcentral.com/1471-2148/12/45>
- [25] Kryukov A.P. The modern species concepts and the role of Russian biologists in their development // *Problemy evolutsii*. Vladivostok: Dalnauka. 2003; 5 31-39. [in Russian, English summary]
- [26] Kryukov A.P., Gureev S.P. New data on interrelations of red-backed and brown shrikes (*Lanius collurio* and *L. cristatus*, Aves) in zone of sympatry // *Zoologicheskyy zhurnal*. 1997; 76 (10) 1193-1201. [in Russian, English summary]
- [27] Kryukov A., Suzuki H., Haring E. The Phylogeny and evolutionary history of corvids // *Natural history of crows*. Sapporo. 2010; 3-19.

- [28] Kulikova I.V., Zhuravlev Yu.N. Molecular-Genetic Studies of Anatinae Interspecies Hybridization from the Example of *Anas platyrhynchos* Susraspecific Complex // *Uspekhi sovremennoi biologii*. 2009; 129 (2) 162-163. [in Russian, English summary].
- [29] Lyubarsky G.Yu. Archetype, Style, and Rank in Biological Systematics. Moscow.: KMK Scientific Press; 1996 [in Russian, English summary].
- [30] Lyubishev A.A. The problem of whether// Problems of form, systematics and evolution of organisms. Moscow: Nauka; 1982 [in Russian, English summary].
- [31] Marova I.M., Fedorov V.V., Shipilina D.A., Alexeyev V.N. Genetic differentiation and vocal in hybrid zones songbirds: Siberian and European Chiffchaff (*Phylloscopus collybita tristis* и Ph. (c.) abietinus) in the southern Urals // *Doklady Akademii Nauk*. 2009; 427 (6): 848-850. [in Russian].
- [32] Martin G. Birds in double trouble// *Nature*. 1996; 380 666-667.
- [33] Masello J.F., Quillfeldt P., Munimanda G.K., Klauke N., Segelbacher G., Schaefer H.M., Failla M., Cortés M., Moodley Y. The high Andes, gene flow and a stable hybrid zone shape the genetic structure of a wide-ranging South American parrot // *Frontiers in Zoology*. 2011; 8 1-16. <http://www.frontiersinzoology.com/content/8/1/16>
- [34] Mayr E. Zoological species and evolution. Moscow: Mir.; 1968 [in Russian, English summary].
- [35] Matute D.R., Butler I.A., Turissini D.A., Coyne J.A. A Test of the Snowball Theory for the Rate of Evolution of Hybrid Incompatibilities // *Science*. 2010; 329 1518–1521.
- [36] McDonald D.B. Microsatellite DNA evidence for gene flow in neotropical lek-mating long-tailed manakin // *Condor*. 2003; 105 580–586.
- [37] Mina M. V. Evolution of Species Concept from Darwin to Our Days: Progress or Wandering? // *Charles Darwin and modern biology. Proceedings of the International Academic Conference 21–23 September, 2009*. Saint-Petersburg: Nestor-Historia; 2010 228-236. [in Russian, English summary].
- [38] Moore W.S. Random mating in the northern flicker hybrid zone: implications for the evolution of bright and contrasting plumage patterns in birds// *Evolution* 1987; 41 539-546.
- [39] Moore W.S., Graham J.H., Jef T. P. Mitochondrial DNA Variation in the Northern Flicker (*Colaptes auratus*, Aves)// *Mol.Biol. Evol.* 1991; 8 (3) 327-344.
- [40] Mora C., Tittensor D.P., Adl S., Simpson A.G.B., Worm B. How many species are there on Earth and in the Ocean? // *PLoS Biology*. 2011; 9 (8) 1-8. <http://www.plosbiology.org/article/info:doi/10.1371/journal.pbio.1001127>
- [41] Morrow E.H., Pitcher T.E., Arnqvist G. No evidence that sexual selection is an 'engine of speciation' in birds // *Ecology Letters*. 2003; 6 228-234.

- [42] Nazarenko A.A. Is unified conception of species in ornithology possible or not? (Opinion of practicing taxonomist) // *Zhurnal obshchei biologii*. 2001; 62 (2) 180-186. [in Russian, English summary].
- [43] Newton I. The speciation and biogeography of birds. Academic Press, Cambridge; 2003
- [44] Panov E.N. Natural hybridization and ethological isolation in birds. M.: Nauka; 1989 [in Russian, English summary].
- [45] Panov E.N. Wheatears of Palearctic: ecology, behaviour and evolution. M.: KMK Scientific Press; 1999 [in Russian, English summary].
- [46] Parchman T.L., Benkman C.W. Britch S.C. Patterns of genetic variation in the adaptive radiation of New World crossbills (Aves: *Loxia*) // *Molecular Ecology*. 2006; 15 1873-1887
- [47] Pavlinov I.Ya. The species problem in biology – another look // *Trudy ZIN*. 2009; 313 (1) Suppl. 250-271. [in Russian, English summary].
- [48] Pavlov D.S., Lupandin A.I., Kostin V.V. Mechanisms downstream migration of young river fish. M.: Nauka; 2007. [in Russian, English summary].
- [49] Price T.D., Bouvier M.M. The evolution of F_1 postzygotic incompatibilities in birds // *Evolution*. 2002; 56 (10) 2083-2089.
- [50] Price T.D. *Speciation in Birds*. Roberts & Company Publishers, Greenwood Village, Colorado; 2008
- [51] Randler C. Avian hybridization, mixed pairing and female choice // *Animal Behaviour*. 2002; 63 (1) 103-119
- [52] Rasnitsyn A.P. On the species and speciation // *Problems of evolution*. Vol.IV. Vorontsov N.N. (ed.). Nauka Press, Novosibirsk. 1975; 221-230. [in Russian, English summary].
- [53] Servedio M.R., Noor M. A.F. The role of reinforcement in speciation// *Annu. Rev. Ecol. Evol. Syst.* 2003; 34 339–64
- [54] Severtsov A.S. The modern species concepts // *Bull. MOIP. Biological Series*. 1988; 93 (6) 3-14. [in Russian, English summary].
- [55] Severtsov A.S. Possible microevolutionary consequences of the hierarchical organizations in vertebrates populations // *Zoologichesky zhurnal*. 2003; 83 (2) 109-118. [in Russian, English summary].
- [56] Shamoni M., Barbash D.A. The Genetics of Hybrid Incompatibilities // *Annu.Rev.Genet.* 2011; 45 331–355
- [57] Shchipanov N.A. Aspects of sustainable persistence of small mammals population stability // *Uspekhi sovremennoi biologii*. 2000; 120 (1) 73-87. [in Russian, English summary].

- [58] Shchipanov N.A. Population as a unit of species existence. Small mammals // Entomological Review. 2003; 83 142-160.
- [59] Shilova S.A. Population Ecology As a Basis for Small Mammal Population Control M.: Nauka; 1993. [in Russian, English summary].
- [60] Short L.L. Hybridization in the flickers (Colaptes) of North America// Bull. Am. Museum Nat. Hist. 1965; 129 307-428.
- [61] Uy J.A.C., Stein A.C. Variable visual habitats may influence the spread of colourful plumage across an avian hybrid zone // J. Evol. Biol. 2007; 20 (5) 1847-1858.
- [62] Warren B.H., Bermingham E., Bourgeois Y., Estep L. K., Prys-Jones R. P., Strasberg D., Thébaud C. Hybridization and barriers to gene flow in an island bird radiation // Evolution (USA). 2012; 66 1490-1505.
- [63] Wirtz P. Mother species - father species: Unidirectional hybridisation in animals with female choice // Animal Behaviour. 1999; 58 1-12
- [64] Zavorsin G.A. Biodiversity as part of the Biosphere-Geosphere System of order out of chaos // The methodology of biology: new ideas. Synergetics. Semiotics. Coevolution. Moscow: Editorial URSS. 2001; 151-176. [in Russian, English summary].
- [65] Zink R. The role of subspecies in obscuring avian biological diversity and misleading conservation policy// Proc. R. Soc. Lond. B. 2004; 271 561-564