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Edited by T.M. Turpaev
N.K. Koltzov Institute of Developmental Biology,
Russian Academy of Sciences, Moscow

Part 3

Reasoning in Birds
by Z.A. Zorina

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(Continued on the inside back cover)

REASONING IN BIRDS

CONTENTS

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REASONING IN BIRDS

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ABSTRACT

Data on reasoning in birds, as vertebrates with a special type of brain structure (progressive development of the hyper- and neostriatum nuclei instead of the neocortex), are discussed in relation to the problems of evolutionary prerequisites of human thinking. To this end, we analyzed the results of our studies carried out on two avian groups – *Corvidae* and *Columbiformes* which are drastically different in both the extent of brain differentiation and in the behavioral patterns displayed in the wild. A classification of the types of reasoning revealed, to date, in vertebrates is proposed, and used as a basis to develop set of tests for comparative studies. *Corvidae* were shown to be, to a certain extent, capable of solving virtually all kinds of reasoning tests, whereas pigeons could only solve two of these tests and their performance is quite poor. A comparison of birds with mammals suggests that, despite drastical dissimilarity in brain structure, the *Corvidae* level of reasoning is close to that of *Cercopithecidae*. Control experiments and lesions of some brain compartments revealed striking differences in mechanisms underlying problem-solving and learning abilities. Tests on crows of different ages revealed a much later appearance of reasoning ability in their ontogeny (no earlier than in one-year-old crows) compared to their capacity for learning (up to its most complex forms) and the species-specific behavioral patterns ensuring survival in their natural environment (3–4 month old). The possibility of correlating of such onset timing with certain attributes of cephalization (degree of myelination of the brain conductive tracts, numerosity of neuroglial complexes) is discussed. We also consider some data which indicate that a high level of cognitive ability in *Corvidae* is also reflected in certain species-specific pattern of behavior and some types of learning. This review also discusses the relationships between the level of reasoning development and the behavioral plasticity of birds in their natural habitats.

KEYWORDS: reasoning, problem-solving, ontogeny, numerical competence, cognition, crows, hyperstriatum.

1. INTRODUCTION

Nowadays, ever increasing recognition and experimental evidence is being given to the concept that animals may have certain behavioral characteristics antecedent to human thinking. This concept was first announced by Darwin in 1872 (Darwin, 1972) and supported by other evolutionists (Severtzov, 1922). Since the experiments of W. Köhler (1925), who was the first to provide evidence of thinking in apes various approaches to their investigation have been developed which have made it possible to establish that not only anthropoids but other vertebrates too possess certain premise of thinking – such as the ability to perceive novel relationships in new situations as well as the capabilities of concept-formation (Erachtin, 1990; Gardner and Gardner, 1985; Köhler, 1956; Krushinsky, 1990; Ladygina–Kohtz, 1965; Maier and Schneirla, 1935; Mackintosh *et al.*, 1985, 1988; Premack, 1978, 1983; Rumbaugh and Pate, 1984; Terrace, 1984, 1985).

Investigation of the reasoning or thinking in birds is interesting because they evolved quite independently and their brain structure is essentially different from those of mammals. The function of the neocortex is performed in birds by a special structure – hyperstriatum, which is nonexistent in mammals (Ariens Kappers *et al.*, 1936; Bogoslovskaya and Polyakov, 1981; Karten, 1969; Krushinsky *et al.*, 1985).

To date, few studies of reasoning in birds have been reported in either Russia and other CIS countries, or abroad. O. Köhler *et al.* (1956) have provided evidence that crows and parrots have high levels of development of nonverbal thinking manifested as an ability for numerical concept-formation. Numerous studies (see the review by Zorina, 1990) have revealed that birds have the ability to acquire several types of concepts: same/different, dimensionality, novelty, symmetry, etc., which are more advanced in Corvidae (Mackintosh *et al.*, 1985; Wilson *et al.*, 1985*a*, *b*). It has also been shown that birds are capable of learning – set formation (Kamil, 1985) and other types of rule-governed learning. Pepperberg's comprehensive studies of the cognitive abilities of grey parrot, which have been underway since the 1970s, have demonstrated that they possess an extremely high level of reasoning.

Another aspect of reasoning in birds – their ability to problem solving in new situations – has been studied in Krushinsky's laboratory in Moscow State University for over three decades after (1958).

2. KRUSHINSKY'S THEORY OF PHYSIOLOGICAL AND GENETIC MECHANISMS OF REASONING

2.1 Theoretical foundation, working Definitions and Methods

Krushinsky in his papers published in 1958–1990 years (see also Poletaeva, 1995) developed and put forward a working definition of animal reasoning which reflected specific features of his methodological approach to this problem. According to his definition, reasoning is the ability of an animal to apprehend simplest empirical laws or rules connecting objects and events in the environment and to apply this knowledge to plan responses in new ways without previous learning or some genetic program. In this context it should be emphasized that we consider those situation in which the animal has no ready inherited problem-solving program or that previously developed by learning. We mean those problem situations which cannot be resolved by a logical way, i.e. on the basis of mental processing of the current informations which do not require preliminary trial and error for the achievement of an adaptive result.

In general, this definition is quite compatible with those of human thinking as defined by psychologists (Luria, 1966) and zoopsychologists (Ladygina–Kohtz, 1965). However, in this definition and the ensuing experimental approaches, the emphasis is placed on the use of concepts of empirical, i.e. natural laws accessible to an animal in its habitat. Krushinsky mean the following simple empirical laws: object permanence, rules of their movement, and geometric properties under which an animal has to operate in the wild and which may compose a sort of cognitive map. On this basis, several experimental procedures have been developed for an evaluation of various types of reasoning. These tests involve the use of various simple logical rules.

The hypothesis of empirical laws, which form the basis of elementary logical problem solving has been developed and was first announced by Krushinsky in 60th years (see Krushinsky, 1965; 1973). In his later work, Krushinsky (1990) pointed out that the above laws do not embrace the entire diversity of empirical laws performed by animals in natural habitats. Particularly, he supplemented this list with temporal and numerical attributes of the environment, though he did not develop respective tests. In subsequent work he proposed a hypothesis on neurophysiological mechanisms underlying the perception of empirical laws. At the present time, the notion of internal representation, such as permanence of objects which have disappeared outside the subject's view, their movement, temporal, spatial and numerical properties, as well as neurophysiological mechanisms underlying them are being thoroughly developed by both Russian and Western investigators (see, for example, 1989; Beritov, 1975; Gallistel, 1989; Natishvili, 1987).

Krushinsky also has supposed that the trend in evolution of reasoning ability was the increase of the number of elementary logical problems which an animal of given taxonomic group cap able to solve in new situations. Therefore, only the use of set of reasoning tests makes it possible to evaluate the general level of heuristic abilities of the brain of animals belonging to various taxonomic groups. Similar viewpoints were later announced by Warren (1977) and Rumbaugh and Pate (1984).

Several elementary logical tests requiring the use of the above "empirical" laws were designed in Krushinsky's laboratory for experimental studies of animal reasoning. These included:

1. Tests based on the extrapolation of the direction of movement of a food bait disappearing from the animal view (corridor test, screen test, etc.; see Krushinsky, 1990).
2. Tests based on operation with geometric characteristics of objects (dimensionality problem, test with two 3-dimensional objects).
3. Tests based on numerical competence in animals, (test on relative numerousness judgment in a new situation).

Let us consider briefly the results provided by these techniques.

2.2 Tests Based on Apprehending of Movement Laws: Test on Extrapolation of the Movement Direction of a Food Bait Disappearing from the Bird's view

The so-called "screen test" was used in the most of experiments. In this test a hungry bird is placed before an opaque screen, 1 m high and 2 m long, behind which two food-cups can be moved. Through a narrow vertical slit at the center of the screen the bird can peck at the food bait for a few seconds; then both food-cups, full and empty, begin to move in opposite directions and disappear after 3–5 s behind little opaque screens so that the bird cannot see further movement of the cups. To solve this problem the bird must realize that the food bait, which has disappeared from its view, continues to move in the same direction as before, i.e. to perform extrapolation of the movement direction of the invisible food bait and, basing on this knowledge to go round the respective side of screen. The bird's ability for extrapolation is estimated according to the result of the first presentation of the test.

The first studies of animal reasoning were carried out by Krushinsky in the late 1950s when this topic of researches did not exist in both this country and abroad. Interestingly, besides tests on dogs, the first studies were carried out on birds – *Corvidae* and *Galiformes* (Krushinsky, 1958). Later a wide range of species from nearly all the vertebrate classes were studied, this was actually the first instance of comprehensive comparative studies of reasoning in animals. It was shown that some elements of reasoning are inherent not only in apes, as previously presumed, but also in representatives of almost all taxonomic groups. The ability for extrapolation is totally absent in fishes and amphibians, but is found in reptiles. Among mammals this problem was most successfully solved by *Carnivora*, and among rodents and *Lagomorpha* – by Norway rats and mice with the Robertsonian-type translocation (Krushinsky, 1990). Subsequent studies with other experimental procedures showed that the ability for extrapolation is also characteristic of primates (Firsov, 1977; Gillan, 1982) and dolphins (Fless and *et al.*, 1987).

Studies of avian species also revealed strike differences in the abilities of birds to solve this reasoning test. Upon first presentation only crows were found; in most cases, to search for disappeared food on the appropriate the side of screen, i.e. they were able to extrapolate the direction of movement of the food-cup after its disappearance from the bird's view. All other bird species studied – domestic chickens, pigeons, ducks, birds of prey – searched for food-cup at random upon the first trial or did not search it at all ("refusals") Repeated presentations confirmed these results. In repeated presentations the *Corvidae* continued to solve the above problem correctly, although some birds did develop perseverance. In other bird species the number of correct choices gradually increased, whereas in individual domestic chickens and the honey buzzard (*Pernis apivorus*) it became predominant.

Hence, despite strike differences in the brain structure of birds and mammals (the absence of the neocortex in the former), the avian class is characterized by the same degrees of extrapolation ability as the mammals. *Corvidae* are characterized by the most developed ability for extrapolation, domestic chickens and pigeon-by the poorest ability, whereas birds of prey occupy the intermediate position. These findings are consistent with the earlier inferences of Köhler (1956) based on his studies of nonverbal thinking in birds using the numerical competence model. In subsequent years, analogous data were provided by studies of other aspects of reasoning in birds – acquiring and transfer of concepts (Mackintosh *et al.*, 1985; Wilson *et al.*, 1985*a*, *b*) and learning-set formation (Kamil, 1988; see also the review by Zorina, 1990).

2.3 *Neutral Regulation of Reasoning in Birds*

In relation to the ability for extrapolation revealed in birds and differences in the extent of its development in various avian species, it appeared important to find out to which peculiarities of the brain structure these distinctions are due and what specific brain regions are responsible for their manifestation. As mentioned above, birds are characterized by their own structural version of the telencephalon which is not analogous to that of mammals. However, despite differences in the spatial organization of the neural networks of hyper- and neostriatum in birds and the neocortex in mammals, their development in the course of evolution rests on the same morphological processes. The studies of Bogoslovskaya and Polyakov (1981) showed that the morphological progression of all lines of brain evolution in higher vertebrates is based on the same principles which are manifested at both the anatomic level and the tissue and cell levels of the brain structure. Electrophysiological studies of the avian brain also indicate that all birds have the same systems of perception, transduction and processing of information as those found in mammals (Morenkov, 1985).

It has been suggested that the complex of hyperstriatum nuclei in birds is the functional analog of the neocortex (Karten, 1969), and part of this complex (the so-called "Wulst") appears to correspond, according to its functions, to the prefrontal area of neocortex (Pasternak, 1977). It was shown that the relative volume of this compartment (Stingelin, 1958; Bogoslovskaya and Krushinskaya, 1975; Voronov, 1989) and the degree of differentiation of its neurons (Dobrokhotova, 1981; Obukhov and Lobanova, 1986) display a progressive increase within the limits of avian class. Therefore, in order to identify the brain structures which regulate the ability for extrapolation and other forms of reasoning in birds, the above-mentioned brain areas was lesioned in: (*a*) crows – birds with a high ability for extrapolation and (*b*) domestic chickens – birds with a poorly developed ability for extrapolation.

The experiments showed that the "Wulst" lesion causes nonspecific changes, common to both species, in their behavior when trying to solve the extrapolation problem – an increasing number of "refusals" to solve the problem and chaotic movements near the screen without passing round it duringthe1min control time. The domestic chickens maintained their chance performance with gradual increase in the number of correct solutions (Fedotova and Zorina, 1985). In contrast, the high level of correct solutions characteristic of crows was lost even when solving a simplified version of the problem – shortening the screen length (Zinovieva and Zorina, 1976; Zorina and Popova, 1976; Zorina and Fedotova, 1981). It is significant that another type of reasoning – dimensionality problem solving, in the same birds was not damaged.

Lesions of the archicortex provided the opposite result: in domestic chickens (poorly solving this problem) the gradual increase in the number of correct solutions was inhibited, which correlates with numerous data on the role of this structure in the mechanisms underlying learning and memory (Krushinskaya, 1963).

Thus, the findings discussed above indicate that the neural regulation of reasoning in birds can show substantial differences: (*a*) depending on the level of its development in various species (*Corvidae*, *Galiformes*) and (*b*) depending on specific type (*s*) of reasoning within the same bird species.

3. EXPERIMENTAL STUDY OF REASONING (AND OF SOME OTHER FORMS OF BEHAVIOR) IN BIRDS

3.1 *The Research Program*

The above data on the level of reasoning in birds were obtained using a single experimental technique. Whereas, the similarity of the level of reasoning development in crows and Carnivore mammals raised the following question: what extent can such a similarity go and what other types of reasoning are accessible to birds? To answer this question it appeared advisable to carry out a comprehensive analysis of reasoning, as well as some other aspects of cognitive abilities, in birds.

In this work we were guided by the principles of the behavioral analysis formulated by Tinbergen (1963). He wrote that investigation of behavior may be regarded as a full-value analysis only when after the period of observations and descriptions the author tries to answer four possible kinds of questions: what factors regulate its manifestation, what are the ways of its development in the ontogeny and phylogeny and what are its survival value? These questions were fully answered only by the ethologists in the analysis of instinctive (species-specific) behavior. We set ourselves the goal of applying these principles to the investigation of reasoning in birds.

With this in mind, during the first stage of our studies we tried to characterize specific features of reasoning in crows using most of contemporary experimental techniques (Zorina, 1995; see Section 3.2–3.4) with subsequent analysis of the factors which control its performance (Section 5.1) as well as specific contributions to survival value (Sections 5.3, 5.4).

To characterize the evolutionary aspects of this type of cognition we compared the levels of its development in representatives various taxonomic groups differently distant from each other (birds and mammals of different species; Section 5.2). In developmental studies of reasoning one can consider, as the initial step, the data on the timing of the onset of various types of reasoning during postnatal onthogeny in comparison with those of certain learning patterns and species-specific reactions (Sections 4.1–4.3). These data are discussed in respect with developmental changes in the brain weight, extent of its myelination and cytoarchitectonics during respective age periods (Section 4.4).

We conducted parallel tests on two groups of birds – corvids and pigeons. The former are characterized by a large, finely differentiated brain, high plasticity of all behavioral patterns under natural habitats and polyphagy. Pigeons have a primitively differentiated brain, display stereotypical behavioral patterns and narrow foraging specialization. Krushinsky was among the first to use these two groups of birds for comparative physiological studies of animal cognition. Later studies have demonstrated the efficacy of such an approach (Powell, 1973; Mackintosh *et al.*, 1985; Wilson *et al.*, 1985*a*, *b*).

3.2 *Tests on Geometric Reasoning in Birds.*

3.2.1 Dimensionality Test. The term "dimensionality problem solving" is used to assess the ability of birds to solve problems based on the fact that voluminous food bait can only be placed into a 3-dimensional and not into a "flat" object (Krushinsky, 1968). To solve the dimensionality problem successfully, birds should be able to perform at least the following operations:

1. To represent that the bait, which can no longer be seen, does not disappear at all (object permanence) but can be put into another 3-dimensional object and move with it ("holding capacity" property).
2. To evaluate and then remember the geometric parameters of the objects and bait.
3. Using the vanished bait as a standard, to compare all these characteristics and decide where the bait is hidden.
4. To remove the voluminous object and take possession of the bait.

Like the test on extrapolation ability, this test – based on natural "empirical" laws – was proposed by Krushinsky (1968) and used for investigation of reasoning in dogs. Later, Dashevsky developed a modified technique and designed a set-up applicable to virtually all vertebrates.

Through their studies it has been established that the dimensionality test is nearly always correctly solved by monkeys (Dashevsky, 1972, 1977) and somewhat less successfully by dolphins (Krushinsky *et al.*, 1972). Bears were also found to be capable of solving this problem (Krushinsky, 1990). All other studied predatory mammals could not cope with the problem initially. They acquired to prefer 3-dimensional object to flat ones after many dozens presentations (Krushinsky *et al.*, 1976). These results brought about a substantial correction of the evaluation of reasoning in predators, therefore, it appeared appropriate to investigate the ability of birds to solve the dimensionality test.

Experiments were carried out in 65 *Corvidae*, mainly crows (*Corvus corone corvix, L.*), but also in rooks (*Corvus fruqilequs, L.*) and a few jackdaws (*Corvus monedula, L.*), ravens (*Corvus corax, L.*) magpies (*Pica pica, L.*) and a jay (*Garrulus qlandarius, L.*). All manipulations were performed in a way as close as possible to those previously used in tests on mammals.

The dimensionality test was carried out as follows:

1. A 3-dimensional bait (a food-cup containing mealworm larvae) was shown to a bird placed in the center of the chamber and facing a vertical slit in a transparent screen.
2. The bait was separated from the bird by an opaque screen.
3. Behind this screen (i.e. out of the sight of the bird) the bait was put inside a 3-dimensional object (for example cube) and then placed onto one of the two demonstration platforms.
4. The 2-dimensional "flat" object was placed onto the second platform 2-dimensional figure is the frontal projection of 3-dimensional one (in this case – the square).
5. The opaque screen was removed enabling the bird to see both objects moving in opposite directions. Both objects revolved around their own axis so that the bird could evaluate their dimensional properties, (Figure 3A).

In all tests about 30 pairs of different objects were used. In order to ensure the maximal possible novelty of each trial, all 3-dimensional objects as well as respective 2-dimensional ones differed from each other in color, shape, size and structure. To make the chance of learning difficult, only one pair of objects was presented during each trial. Trials carried out at 2–3-day intervals.

Preliminary tests were conducted in order to check whether the birds were aware of the objects permanence, i.e. the ability to search for the bait disappearing from their field of view, and whether they possess the capacity to represent that voluminous objects can contain other 3-dimensional bodies. For this purpose a bait was placed 60 cm away from the crow and covered with an opaque 3-dimensional object. Another identical 3-dimensional object was put nearby with nothing underneath it. In 90% of cases the crows toppled 1–2 s the 3-dimensional object covering the bait. The successful result continued to be rather high (70 ± 4.45%, $p < 0.01$) if both objects were shifted by 50 cm, such that the empty voluminous one appeared in initial position of the object covering the bait.

Unlike the crows, the pigeons did not try to search for the food covered before their eyes by a 3-dimensional object and could not master this operation even after special "prompts".

Thus, *Corvidae* appear to be capable of operating with the representation the object permanence, of the bait removed before their eyes from the field of view and with the representation of 3-dimensional object capacity to contain other 3-dimensional bodies, *Columbidae* are unable to operate with such representations which makes useless their dimensionality testing. This ability in crows is also supported by their widely known ability of caching and retrieval of food stores. In the Nutcracker (*Nucifraga caryocatactes, L.*) this is the obligatory component of rearing their nestlings, inherent in the entire species. This ability was shown to be based on remembering the exact place of each cache (Kamil and Balda, 1985; Krushinskaya, 1966; Vorobiev, 1982). In other *Corvidae* species this property is not manifested in such a stereotypically way. None the less, our observations indicate that, in all studied species this food-storage behavior is revealed as early as the 6–7th week of age, first in some members of group and then spreading fast among others, possibly in part through imitation (Zorina, 1989). The use of Piager's tests also revealed the object permanence representation in four parrot species (Pepperberg and Kozak, 1986; Pepperberg and Funk, 1990).

Results of the Dimensionality Tests

In the first trial the dimensionality problem was solved by 37 out of 65 birds (57%, $p > 0.05$). According to the established criteria (Krushinsky, 1990), it should have been expected that crows were incapable of this kind of reasoning. However, the predominance of correct solutions upon repeated trials (70%, $p < 0.01$) and, in particular, consideration of the behavioral specificity of individual birds in repeated trials necessitated revision of this notion.

Figure 1 shows typical pattern for solving the dimensionality problem multiple repetition. A proportion of birds (Figure 1*A*, *B*) find correct solutions in the most part of cases, few errors being regularly distributed over all repetitive trials (group of adequate choice, G1). Other birds (Figure 1*C*)

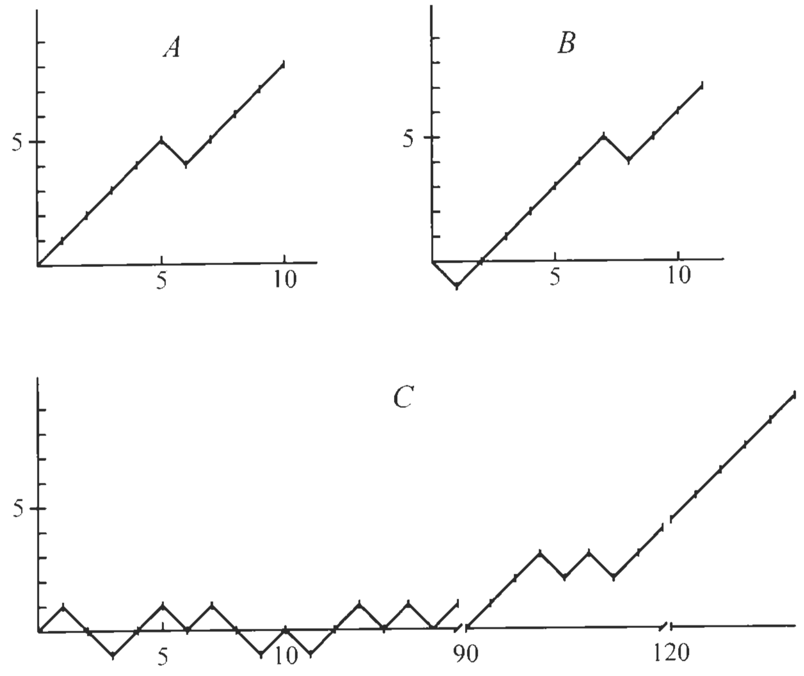

Figure 1. Individual patterns of correct (line direct upward by 45°C) and incorrect (line directed downward) solution of dimensionality test in *Corvidae*. Abscissa, number of trials.

display alternating correct and incorrect solutions, with no definite system or with more or less extended perseverance periods (learning group G2). The share of correct solutions in group G1 ranged from 70 to 100%, exceeding ($p < 0.05$) the average level of correct solutions estimated for all birds studied. In birds referred to group G2, the correct solutions over the entire trial period accounted for no more than 70%.

Comparison of the indices of problem solving by the two bird groups (Figure 2) shows that they differ from each other in all parameters studied: in G1 birds solve the problem at once, whereas in G2 a typical discrimination conditioning occurs.

Species Composition of G1 and G2. Analysis of species composition of groups G1 and G2 shows that representatives of all tested species exhibit virtually the same distribution patterns. Although the number of rooks, magpies, jackdaws and ravens in both groups was insufficient to make definitive conclusions, it may, nevertheless, be suggested that the differences in the behavior of birds in solving this problem are equally characteristic of all tested species and appear to be due not to species differences but to some other peculiarities of their higher nervous activity. The absence of distinctions in the problem – solving ability displayed species sufficiently diverse according to ecology, suggests that our estimates of the reasoning abilities are characteristic of the entire Family irrespective of some particular species' adaptations.

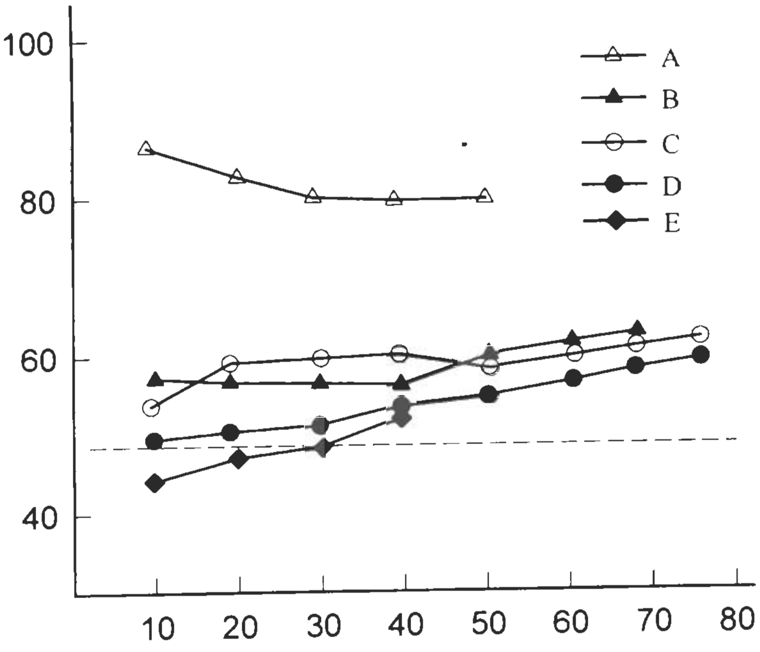

Figure 2. Dynamics of correct choices made by *Corvidae* in trials from 1 to n (n is a multiple up to 10). Dimensionality test: *A*, G1; *B*, G2; *E*, group of 3-month-old birds. Control experiments: *C*, group 3DF+; *D*, group FF+. Abscissa, number of trials; ordinate, percent of correct choices in trials ($1 - n$).

Comparison of the Problem – Solving Mechanism in Birds Referred to as G1 and G2 Groups

To check the hypothesis on the different mechanisms underlying behavioral patterns of birds in the G1 and G2 groups, it appeared appropriate to analyze the experience gained by birds in the process of repeated presentations of this problem. Thus employed the conditional probabilities method

(Ventzel, 1962) which had first been used by Dashevsky (1972) to analyze the results of reasoning tests in animals. This method makes it possible to estimate the results of problem solving in trials (n) depending on the results of problem solving in a previous trial ($n - 1$), i.e. it enables us to reveal the structure of the experience gained in the course of trials. According to our estimates, in group G1 birds the probability of making a correct choice in a specific trial is independent of whether the previous solution was right or wrong; the values of respective probabilities are close to the mean frequency of 3-dimensional object choice. This fits the criterion of independence of events and makes it possible to infer that the G1 group birds try to solve the problem as a new one irrespective of the results of the previous trial. The birds of G2 group display a gradual amelioration of the results due to an increased probability of correct solutions after incorrect choices and a decreased probability of two incorrect solutions in succession, i.e. usual process of discrimination learning.

Thus, group G1 and G2 birds exhibit certain differences of principle as regards their experience benefited in the course of repeated problem solving trials.

Analysis of Latencies (L) of Dimensionality Problem Solving

The data presented in Table 1 show that birds in groups G1 and G2 differ from each other in all the scores studied. Particularly, in G1 birds the mean L of the choice of object is shorter than in G2 birds. In G2 birds the L of correct and incorrect solutions are virtually the same, whereas in G1 birds L of incorrect choices is substantially shorter than the L of correct solutions. In this context, it may be suggested that the G1 group differs from the G2 group not only by a smaller share of incorrect solutions but also by their character: judging by the shorter L, incorrect choices in G1 birds may reflect not the results of decision making (which requires more time) but rather their inability to inhibit the chance impulsive reaction. Thus, G1 and G2 birds also differ in the temporal patterns of problem solving.

Control Tests

The above data indicate that at least a proportion of *Corvidae* are capable of dimensionality problem solving. This raises the question as to whether there occurs a real apprehending of the logic of the test and the ensuing adequate decision making, or whether the choice of 3-dimensional objects is due to some other factors. To answer this question control tests were carried out (Krushinsky *et al.*, 1981) in which the possibility of a logical solution of the problem was ruled out, while preserving most of the external attributes of the experimental design and procedure (Figure 3).

The demonstration platforms were replaced by 4 cm deep food-cups of the same diameter, one of which contained bait to reward the correct choice. Both 3-dimensional and flat objects were rigidly fixed on the lids, which were devised in such a way to make the bird perform the same mental reaction as they did the dimensionality test – solving task. Because of these changes the problem lost the uniqueness of its solution – it was equally probable that the bait could be either in the food-cup covered by the lid with the 3-dimensional figure (3DF – Figure 3*B*) or in the one covered by the lid with the flat figure (FF – Figure 3*C*) (groups 3DF+ and FF+, respectively). All other elements and the protocol accurately reproduced the basic procedure. This technique was first proposed by Dashevsky (1977) to investigate the behavior of monkeys and dogs in solving this problem.

Table 1. Latency (in seconds) of correct and incorrect solving of dimensionality problem in G1 and G2 groups of corvids.

Groups	*Latencies*			*Statistical significance*
	Average	*correct choices*	*incorrect choices*	
G1	17.57 ± 2.01	19.69 ± 2.57	11.9 ± 2.78	$p < 0.05$
G2	25.95 ± 3.19	24.23 ± 2.65	24.3 ± 2.41	$p > 0.05$
Statistical significance	$P < 0.05$	$P < 0.05$	$P < 0.001$	

In such a modification of the control test the behavior of birds was found to be strictly different from that observed in the dimensionality test. As shown in Figure 2 (curves *C* and *D*), during the first tens of trials the birds reacted to the objects in a purely random manner and only gradually began to give preference to the reinforced object. In group 3DF+ this took place on the average, after 30 trials; in group FF+, after 80 trials. Figure 2 (curves *A* and *B*) also shows the accumulation curves of correct solutions in the dimensionality test. It can be seen that the learning curves in groups 3DF+ and FF+ virtually coincide with that in G2 and show a statistically significant distinction from the G1 curve (curve *A*).

Thus, the above tests suggest the following. They provide evidence of the availability of certain perceptive preferences for 3DF which ensures the course of learning in group 3DF+ to be 5–15% more successful. However, its small and statistically insignificant departure from the chance performance level and a drastic difference from the G1 curve indicates that the preference given to 3DF cannot be the mechanism underlying dimensionality problem – solving behavior. Furthermore, these experiments show that the behavioral pattern typical for G1 birds is only possible on

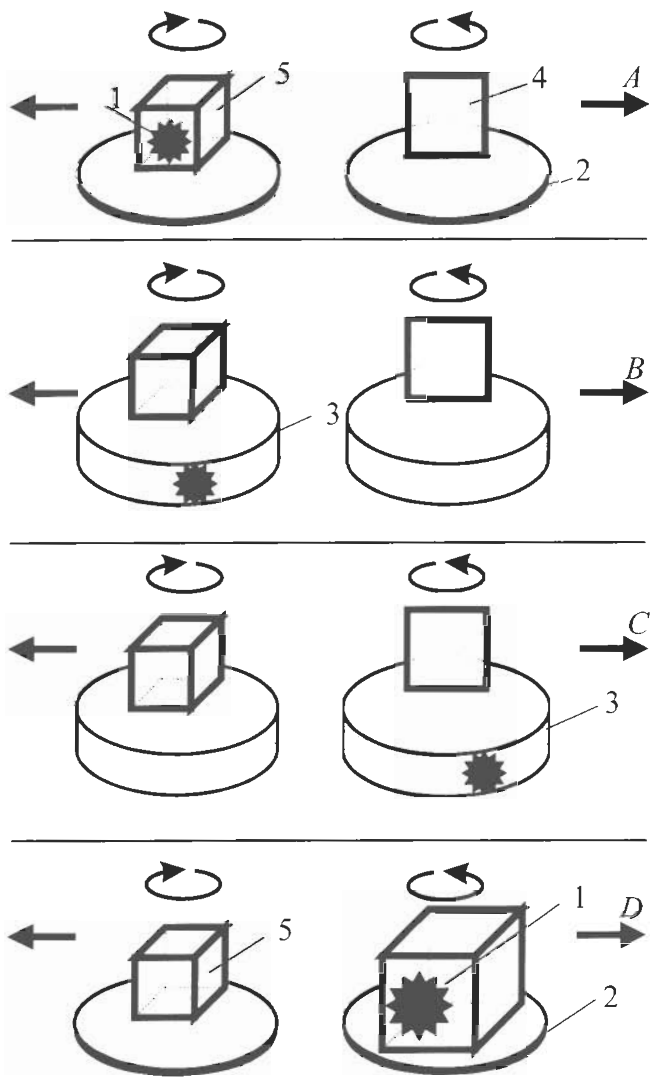

Figure 3. Experimental set-up: Dimensionality test: *A*, control experiments; *B*, positive stimulus is 3-dimensional; *C*, positive stimulus is flat. Test on choice between two 3-dimensional stimuli: *D*: 1, food bait; 2, platforms for supporting stimuli; 3, food-cups for bait; 4, flat stimulus; 5, 3-dimensional stimulus.

solution of logical problems and is ruled out in the discrimination learning situation. On the contrary, the behavior of birds in G2 group totally corresponds to that during typical dimensionality discrimination conditioning. Finally, these data demonstrate the ability of birds to learn the concept "dimensionality" which confirms the high capabilities of *Corvidae* for concept formation reported by a number of authors (see review by Zorina, 1990).

3.2.2 Test with Two 3-dimensional Objects possessing different volumes. Successful testing of *Corvidae* for their ability to solve the dimensionality problem suggested that they are also capable of solving other problems based on the operation of the representation of object permanence and the notion of the "holding capacity" property. For this purpose, we have designed, in cooperation with B. A. Dashevsky, a test using two voluminous objects of the same form and color but which differ substantially in their volumes (Figure 3*D*). Because of the design and despite the fact that both objects possess the capacity to hold other object, only one of them is large enough to contain the food-bait cup. To solve this test, the birds must not only evaluate both objects with regard to their dimensionality, but also make a quantitative comparison of their sizes. In this context, the test with two voluminous objects may be regarded as a combined one requiring the operation of two attributes of stimuli – geometrical and quantitative.

Such tests were carried out on 20 birds of one year-old of age. Depending on their previous experimental experience, they were divided into four groups. The first group contained five birds from G1 which had successfully solved the dimensionality test and had been subjected to no more than 15 trials. The second group comprised five birds from G1 tested for a longer period (30–60 trials). The third group included five G2 birds, of which three demonstrated steady perseverance, whereas the fourth bird acquired correct solutions only after a long period of chance performance. Finally, the birds included in the fourth group not been involved in any preliminary tests. The experimental procedure exactly followed the preceding test protocol.

In the first trial the birds chose both objects with equal probabilities; however, upon repeated problem setting (from six to ten times) they displayed a statistically significant preference for the larger object (73 out of 118 trials, 62%; $p < 0.05$). Based on these results, we might suggest that the correct choices appeared as a result of discriminative learning. However, the use of the single-factor dispersion analysis showed that the result of trial was independent on its ordinal number. Calculation of conditional probabilities revealed no relationship between the results of the given and preceding problem - solving trials.

While solving this problem, individual birds showed considerable variability in their behavioral patterns. So, in 7 out of 20 birds the choice of the larger voluminous object exceeded 70%, with an average of 87% ($p < 0.001$). In five birds the choices of the larger object prevailed, but it was unimportant and statistically insignificant (65%; $p < 0.05$). Four birds demonstrated equal probabilities in the choice of the larger and smaller objects. Finally, two birds displayed preference for the smaller ones.

A comparison of these findings with the results of the dimensionality test revealed their direct interrelationship: the more successful were the birds in the dimensionality test, the better were the results of the test with two voluminous objects. All birds of group 1 chose the larger object in 70% of trials ($p < 0.05$), whereas in group 3 none of the birds exhibited predominance in correct solutions. Despite the fact that not all the birds successful in the dimensionality test could correctly solve the problem with two voluminous objects, none of the birds which failed in the first test could solve the second problem. In this connection, it should be noted that the absence of the dimensionality problem - solving experience *per se* did not rule out the possibility of a correct solution of the problem with two voluminous objects – one bird in group 4 displayed a statistically significant preference for the larger object. Thus, the *Corvidae* are able to solve the test with two 3-dimensional objects of different volumes which requires the operation of both the geometrical and quantitative attributes.

Summing up the results of the two sets of tests it may be concluded that the *Corvidae* are capable of the following types of reasoning: in new situations they make use of the following empirical laws – the representation of object permanence and the capacity of one voluminous object to contain another one ("holding capacity"). They differ, however, from other studied vertebrates by the existence of two independent behavioral patterns in the process of this problem solving which are distinct with regard to all studied parameters.

As mentioned above, the supposed mechanism underlying the solution of this test is the mental comparison of dimensionalities of two objects available at the moment of choice and the memorial representation about dimensionality of food-bait (it serve the standard for comparison) which is absent at the moment of choice (Dashevsky, 1977). The differences we revealed in the duration of latencies suggest that there is an optimal duration of the decision-making process; by reducing the latencies the solution may prove to be incorrect, but increasing the latencies *per se* does not necessarily ensure a correct outcome. The test with two 3-dimensional objects, of which only one can contain a voluminous bait, also support the operation of the above decision-making mechanism. Indeed, as regards the dimensionality test, it might be suggested that a sort of spontaneous matching-to-sample takes place according to the following pattern – a voluminous object is chosen as a stimulus matching to a voluminous bait, although the crows are known to require a sufficiently large number of trials in this type of learning (Mackintosh *et al.*, 1985; Wilson *et al.*, 1985*a*, *b*). As far as the test with two voluminous objects is concerned, such an assumption is absolutely inadmissible because solving this test requires not only an evaluation of objects' dimensionality but also a quantitative comparison of their sizes. Since this problem is correctly solved by a smaller proportion of birds compared to the previous test, one may conclude that for birds this represents greater degree of difficulty than the dimensionality test.

3.3 Revecz–Krushinsky Tests

The next stage of our studies involved the use of the test first proposed by Revecz (1925) for the comparative evaluation of reasoning in monkeys and human infants and later developed independently by Krushinsky and Popova (1981) for investigation of the ontogeny of human nonverbal reasoning. Such an evaluation was supposed to be an analog of the extrapolation seemed more appropriate for human studies. In this case, the individual under test is offered a number of food-cups covered with lids. In the first trial, the bait is put into the first food-cup outside the field of view, the bait may be found by removing the lids from the food-cups. The bait is then placed in the second food-cup, third food-cup, and soon up to twelfth. Finding the bait in the first and second food-cups provides the necessary and sufficient information in order to determine the rule of further bait shift. For this, it is necessary to perceive the relationship between the place of the bait in the preceding trial ($n - 1$) and its position in the given trial (n) in order to draw a conclusion as to where the bait will be positioned in the next ($n + 1$) and subsequent trials.

In the contrary to the above-considered extrapolation and dimensionality tests which are based on the objective properties of the environment and have a single solution, in this situation the rule of the bait shift is set arbitrarily by the experimenter (the shift direction and its step may be changed). This test have no direct analogs in the natural behavioral repertory of birds, but, as reported by Kamil (1978), at least some bird species possess a necessary volume of working memory. It was shown that *Loxops virens* feeding on the nectar of apricot trees visits groups of flowers in a

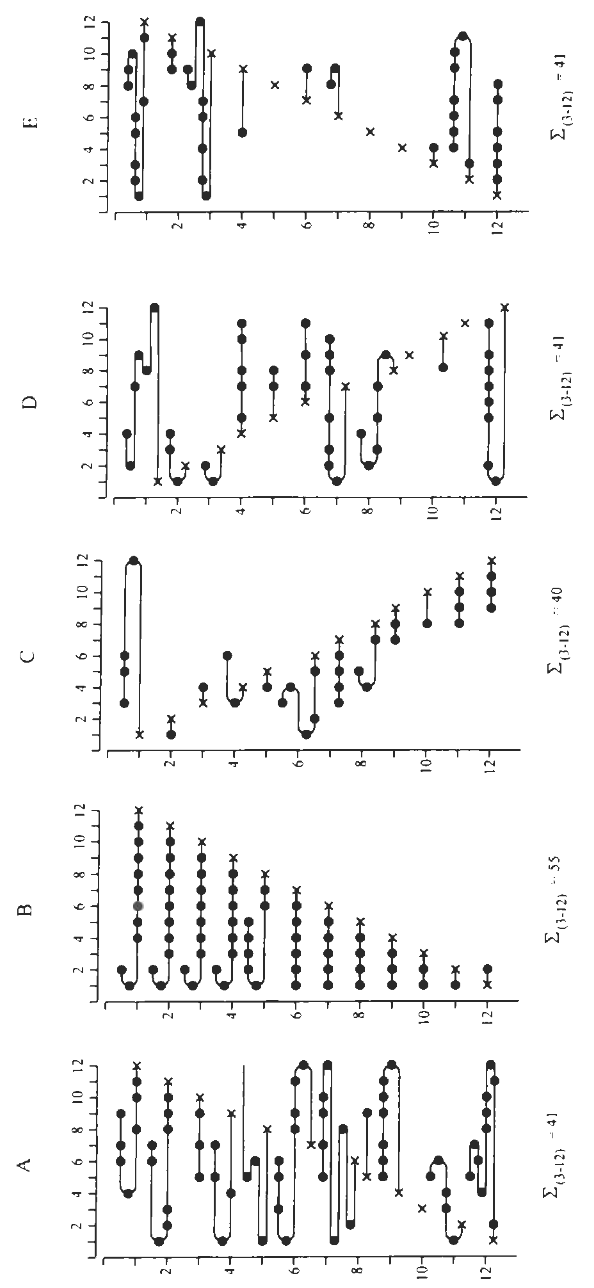

Figure 4. Patterns of bird behavior in Revecz–Krushinsky test (*A D*). Explanations in the text. Abscissa, number of food-cups; ordinate, number of trials.

definite order, returning to them only after sufficient time for the accumulation of new supplies of nectar.

Numerous studies have demonstrated a high efficiency of this test in the evaluation of human nonverbal thinking. Particularly it has been shown that the development of ability to solve this problem accounts for a long period in human ontogeny; only after 15 years of age does it reach the level characteristic of the adult population (Krushinsky and Popova, 1981).

We carried out this test on 2 pigeons and 48 Corvidae of the above-mentioned species, but mostly crows (Krushinsky and Zorina, 1982; Zorina, 1982; Zorina and Salimov, 1989). Grazhdankina tested 17 monkeys and 6 apes of different species and their performance were compared with those of Corvidae (Zorina *et al.*, 1988).

Each test consisted of 12 trials with the food bait placed successively in each food-cup. The correct solution was to find the bait at once after opening 1–2 empty food-cups (the so-called "incomplete solutions"). The criterion of comprehending the rule of bait shift was three and more correct solutions in succession.

Figure 4 shows patterns of typical behavioral strategies of *Corvidae* in the process of problem solving. Apparently, some of the birds did not comprehend the rule of the food-cup shift at all, and their performance remained purely occasional in all 12 trials (Figure 4*A*). Some birds combined the chance performance with the so-called "stereotype" search, when the bird opened successively all adjacent food cups in a row before it found the bait (Figure 4*B*). A certain approximation to the appropriate performance can be seen in Figure 4*C*. In this test, although the bird did not determine the exact location of the bait, it certainly accounted for the shift of the food. In any case, the zone of search gradually narrowed and shifted with the bait shift. Such birds also displayed 1–2 correct choices, but these were separated by periods of chance performance.

Figure 4*D* shows an example of the most successful test solution – three successive correct choices of the bait displayed by only a few birds. Additionally, a number of birds reached another criterion – three and more successive correct choices of the bait after 1–2 mistakes (Figure 4*E*). The same behavioral patterns were revealed in both apes and monkeys, their scores exhibiting no significant differences in *Corvidae* and between both groups of primates.

Since the above strategies of the food-bait search were characterized by different degrees of deviation from the chance performance and the narrowing of zone of search it appeared advisable to estimate the statistical significance of the decrease of the number of attempts preceding the loca-

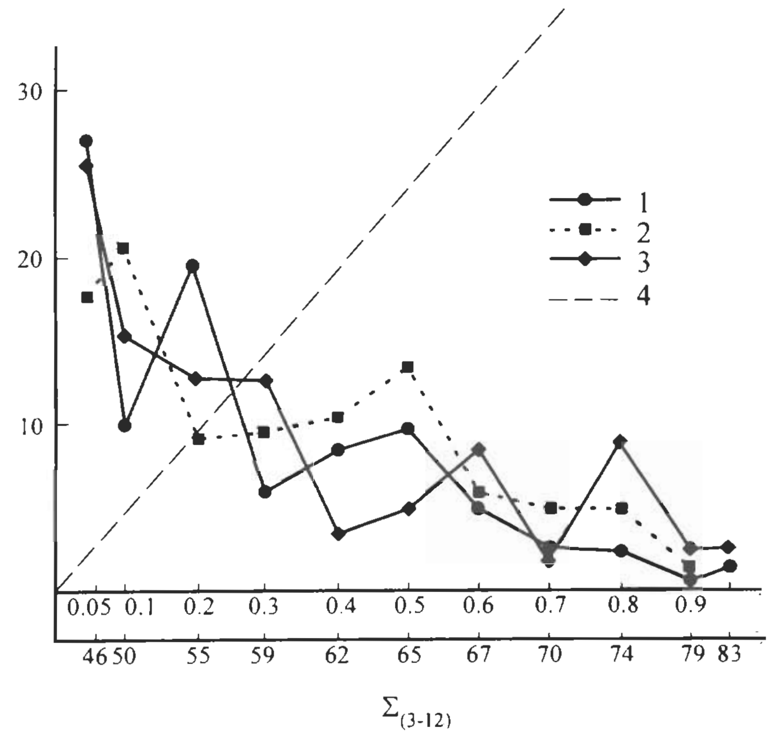

Figure 5. The distribution of Revecz–Krishinsky test solution parameters in *Corvidae* (1), monkeys (2) and apes (3) as a function of probability of chance performance of this sum of trials. Abscissa: p, probabilities. $\Sigma_{(3\text{-}12)}$, general sum of trials, performed during 10 presentations of food bait. Ordinate number of subjects (%) performed this number of trials.

tion of the food. Hence, we summarized all attempts made during the search for the bait in all the trials (from the 3rd to the 12th) and carried out statistical analysis using the "random wandering" model developed by Salimov (Zorina and Salimov, 1989). This model was used to calculate the probability of random achievement of the same number of attempts upon "random wandering" and to plot the distribution curves of the said magnitudes for *Corvidae* and both groups of primates. As shown in Figure 5, in 34% of all tests this number was significantly smaller than the number performed at "random wandering". This score differs from the theoretically predicted one at $p = 0.0007$ (the accurate method of Fisher). On the contrary, in two birds (4.1%) the number of attempts was maximum – from 49 to 72. As can be seen from the graph, the low-probable decreased values of this parameter were found much more frequently than the values characteristic chance performance, and the curve of their distribution is drastically different from the theoretical one. Interestingly, as regards this index, the *Corvidae* and the primates of both groups do not differ absolutely.

Tests in Pigeons

The behavior of pigeons in this test essentially differ from that of *Corvidae*. As in the tasks described above, the pigeons did not try to search for the bait in closed food-cups. In order to force them to open the food-cups, a grain of wheat was glued to the edge of each lid. However, after opening a few food-cups at long time intervals, they gradually stopped searching at all, they never opened all 12 food-cups in succession or revealed any indication of apprehending rule of bait shift. The total absence of purposefulness in the behavior of these birds made the continuation of such tests pointless.

The data discussed above provide evidence that at least some *Corvidae* solved the given test, i.e. in a new situation they are capable of grasping the pattern rule of further shift of the food bait on the basis of information derived from the first trials. For this, they must apparently, retain the results of at least two preceding bait locations and use them as a basis for mental comparison to comprehend the rule of the bait shift and extrapolate its probable position in the next trial. Davis and Perusse (1988) suggested that solving of this test are based on the number of food cups in the total series. They considered these data in relation to the numerical competence of animals; this assumption, however, appears to us to be insufficiently substantiated.

Comparison of the results of problem solving by birds and primates revealed no substantial differences in their behavior (Zorina *et al.*, 1988). This is supported by the above-mentioned data on the similarity of reasoning levels in *Corvidae* and monkeys (Kamil, 1988; Krushinsky *et al.*, 1979, 1982; Zorina, 1982).

3.4 Tests on the Integration of Previously Acquired Isolated Experiences

It is commonly accepted that one of the types of reasoning in animals is their ability to integrate the previous experiences in order to perform a new act in a new situation which does not rely on a particular behavioral element. Such behavior is not a trivial transfer of previously acquired isolated experiences into a new situation, because memory is used not to provide some previously formed programs of reactions but to provide the information required for developing new programs. This approach to studies of reasoning, which is widely accepted nowadays (Ellen and Anschel, 1981; Epstein, 1987), was proposed by Maier and Schneirla (1935) and formed the basis for first experimental studies of reasoning in vertebrates other than primates. Two experimental tests of this kind of reasoning were developed in Krushinsky's laboratory.

3.4.1 "Cooperation" Test. The "cooperation" test devised by Bondarchuk (Krushinsky *et al.*, 1982) consists of the following. Two crows were taught to cooperate for obtaining food by synchronously key-pecking in two neighboring Skinner boxes separated by a transparent partition. In parallel and independent tests some of them were taught to open the bait-containing cage which was closed from the outside. When one of the two crows was locked in the cage, the behavior of the second, "free", crow was observed. In order to get reinforcement for key-pecking the "free" crow had first to open the cage and release its partner.

In the experiments on eight pairs of hooded crows a fairly uniform picture was observed: in the first four to eight trials the "free" crow opened the cage in 50% of cases. Then a crucial change in behavior occurred, the partner was released in virtually all cases irrespective of the box cage in which it was locked. If the behavior of the free crow in the first trials could still be regarded as solving the problem by trial and error, then the dramatic shift to the correct strategy might be considered to be a manifestation of immediate decision making based on an assessment of the situation.

3.4.2 Test on Immediate Comparison of Stimuli Previously Related to Different Number of Reinforcement Items: Choice under the control of "More than" Concept. This test was developed in studies of numerical competence in birds (Zorina *et al.*, 1991). During the process of learning animals appeared to acquire information about the number of reinforcement items while the experimental procedure was not structured to force them to acquire this information. This is also evidenced by the fact that changes in the degree of reinforcement make it possible to control the spatial learning (Riabinskaya and Ashikhmina, 1988), including deficit of previously acquired reaction when the level of reinforcement was dramatically reduced. It is also known that most animals, when offered a free choice, prefer stimuli which are larger in both absolute magnitude and the number of elements in a set.

Based on this information, we proposed a test that required an immediate evaluation and comparison of two sets of food items by a bird finding itself in a new situation. The test consists in the following.

In the process of preliminary training birds acquire several isolated simple instrumental conditioned reactions – to open the food-cup in order to receive the reinforcement. In the course of such training birds acquire also information that definite numbers of reinforcement items (from one up to eight) correspond to food-cups of different colors. Upon completion of preliminary training we carried out a test in which the food-cups were presented in pairs in different combinations (a new situation for the bird). We then checked whether the birds would prefer the food-cup previously associated with a higher level of reinforcement and to see the limits within which they would make such a choice. In our view, the behavior of birds solving this test fits the definition of Maier and Scheirla (1935), since the correct reaction requires integration of elements of memorial representations from previous isolated experiences – to compare the number of reinforcement items pertaining to each food-cup and to perform a novel solution – to choose the greater reinforcement.

Tests were carried out on six pigeons and ten crows. We used cylindrical food-cups of different colors covered with lids of the same color. Each food-cup was offered no less than 100 times to pigeons and at least 50 times to crows, with 2–3-day intervals between such series. Each food-cup contained different numbers of reinforcement items: from one to eight wheat grains for pigeons and from five to twelve mealworm larvae for crows. We conducted tests days after training, during which birds were offered pairs of food-cups which were previously shown only individually. Each pair was presented three times with other 20–25 pairs during the entire test. The results obtained indicated that over the entire range of studied sets the birds of both species preferred, on average, the stimulus related to a greater number of reinforcement items (69.9 + 2.6% of correct choices in pigeons and 60.1 + 3.2% in crows). In individual specimens the prevalence of correct over random choices was found to vary rather substantially.

Figure 6 shows the dependence of the proportion of greater reinforcement choices on the absolute difference of numbers reinforcement items under comparison. In pigeons, these scores are seen to be directly proportional. Of interest is the fact that even at levels of reinforcement differing by only one wheat grain the pigeons correctly identified stimulus related to a greater reinforcement in three of the eight test pairs ($p < 0.05$, $p < 0.01$). At greater differences between the compared stimuli, the proportion of such choices was found to increase. In contrast to pigeons, crows were found always to prefer the greater reinforcement without any dependence on the absolute differences between arrays under comparison. Our data revealed that crows performance was successful within the entire range birds were able to reorganize these habits reproducing the behavior pattern of a chimpanzee which placed in a box underneath suspended "banana". It may be suggested that this type of reasoning is the only or one of the few types accessible to pigeons.

3.5 *Numerical Competence in Birds*

The data about bird's capacity to solve the test on immediate comparison of stimuli previously related to different number of reinforcement items (Zorina *et al.*, 1991) present us with challenge of trying to investigate another types of numerical competence in birds.

Our study was performed in two directions: 1) to check the range of numerosities, which the birds can evaluate; 2) to investigate bird's capacity of numerical concept formation.

To check our data mentioned above that the birds can estimate the arrays containing more than seven food items, relative numerousness judgment in free-feeding situation was studied. Six crows and eleven pigeons were presented with different sets of 1–12 food items – meal worms – for crows and 1–10 wheat grain for pigeons. In this experiments two opened cups with sets of food items were presented simultaneously and the bird could eat the food only from the firstly chosen cup on every trial. The data obtained (Zorina and Smirnova, 1994) also supported, that birds tended to choose the greater set in the range up to 12 items, but not up to 7–8, as it was demonstrated earlier (O. Köhler, 1956; Davis Perusse, 1988). In crows this preference was stronger (80.3 + 1.1% choices of greater sets, $p < 0.001$) and manifested itself even under minimum absolute and relative difference (1 item and 0.8 correspondingly), while pigeons choose the greater sets in 58.0 + 1.1% and only under rather significant differences between sets (> 3 items and > 0.5 correspondingly). It has been suppose, that in pigeons the choice is based on the evaluation of cumulative area of the set, while in crows - on the juxtaposition of the number of elements itself.

This hypothesis was tested in the next experiment in numerical concept learning situation. Four crows were trained to choose the greater array from pairs of numerousness discriminanda in the range of "1–12". In the process of training, all irrelevant attributes of the arrays (geometric form, size and color of elements, as well as pattern of their placement) were varied. Several control procedures were employed to make extraneous cues unlikely. In particular, in order to preclude the use of cumulative area or other magnitude cues, ratio of cumulative area of elements to their numerosity was varied. In a half of the presentations the greater array consisted of bigger elements while the lesser array consisted of smaller elements and in the other half the greater array consisted of smaller elements while the lesser array consisted of bigger elements. All crows demonstrated high accuracy of comparisons. They chose the greater arrays in 75.3 + 2.4% including under the minimum difference between the compared arrays. It was concluded that these crows were able to compare the arrays in the range of "1–12" by numerosity itself and to acquire the concept "more, than".

When arrays in the new range of "10–20" were presented, all crows demonstrated successful transfer of acquired concept without any additional training (71.5 + 2.3%). The capacity of this type of numerical concept transfer was never yet known both in birds and mammals. However, when ratio of cumulative area of elements to their numerosity was varied, only two of the four crows performed successfully (71.9 + 3.6%).

When arrays in the new range of "15–25" were presented, one of the crows demonstrated a high level of correct choices (75%) without additional training. However, when ratio of cumulative area of elements to their numerosity was varied, the choice became unstable (varied from 30 to 90% in 10 successive presentations). Most errors were made when the greater array consisted of smaller elements while the lesser array consisted of bigger elements, i.e. the correct choice could only be based on evaluating of the numerical but not another quantitative attributes of the arrays. We conclude that upper limit of the range, within which the crows are able to compare namely numerical attributes of arrays are close to 20. On the whole, these data suggest that crows are capable of "more than" concept learning based on numerical discrimination in the range of up to 20 (Zorina and Smirnova, 1995; 1996 in press).

4. AGE-DEPENDENT DIFFERENCES IN REASONING ABILITIES IN CROWS

There are virtually no data either on the ontogeny of reasoning in birds or on brain development in late postnatal ontogeny. Information concerning development other forms of cognition and brain ontogeny in Corvidae is scanty. Such data are confined to information on foraging (Blinov, 1983; Shutenko, 1980), and social behavior in young birds (Zorina, 1977 1989), early developmental stages of auditory system (Golubeva, see this volume) vocalization (Korbut, 1977) and some other behavioral patterns. Shutenko (1980) reported a comprehensive analysis of the development of foraging, motor, vocal and preening behavior in hooded crows; however, his observations were confined to birds up to 5 weeks of age.

We investigated the age-related peculiarities in crow's ability to solve certain elementary logical problems, as an initial stage of our studies into reasoning ontogeny in birds. Tests were carried out in 3-month-old birds. This age was chosen because of this time the birds have completed the development of foraging behavior. They no longer obtain food from their parents, some broods start to unite and form flocks which makes their social behavior more complex. Our observations of groups of young corvids in captivity revealed that their exploratory (Zorina, 1983), manipulative (Zorina *et al.*, 1986; Deriagina *et al.*, 1988), feeding and social behavioral patterns approach those of adult birds.

4.1 *Complex Learning*

Our literature search failed to provide any information on age-related peculiarities of learning capacities of altricial birds in late ontogeny. Our data (Zorina *et al.*, 1989) indicate that at this age the *Corvidae* already possess a sufficiently developed ability not only for simple instrumental conditioning (including color discriminations) but also for successful performance in a multiple schedule of color discrimination learning. According this schedule birds were trained to acquire four or five color discriminations. During this training birds had to learn that stimuli B, C and D may be both positive and negative, depending on which stimulus they were coupled.

In contrast to B, C and D, stimuli A and F may be only negative and positive, respectively. In addition, the number of reinforcement items related to various stimuli, was from zero to five. Such a schedule system of discriminations ($A^{0}B^{+1}$; $B^{-}C^{+2}$; $C^{-}D^{+3}$; $D^{-}E^{+4}$; $E^{-}F^{+5}$) was used in tests on human infants (Bryant and Trabasso, 1971), apes (Gillan, 1981) and birds (Zorina *et al.*, 1995) as a preliminary stage in evaluating their ability to transitive inference.

Our experiments showed that, as regards the dynamics of the acquiring of multiple schedule of discriminations, the groups of 3- and 12-month-old crows did not differ.

4.2 *Extrapolation Test*

Tests on the ability to extrapolate the direction of movement of a food disappearing from a bird's view were carried out in 17 3-month-old crows (Zorina and Krushinsky, 1987). It turned out that in the first trial the number of correct solutions did not exceed the chance performance level characteristic of such birds, the trajectory of movement in search of food is of a disorderly and chaotic nature. A distinctive feature of their behavior were the "refusals" to solve the problem, i.e. the absence of any solution within 1 min after disappearance of the bait. The number of "refusals" in 3-month-old crows was four times greater than seen in adult birds (48% and 11%, $p < 0.05$). Thus the ability of 3-month-old crows to extrapolation problem – solving appeared to be significantly lower than those of one-year old birds. The data reported by Krushinsky *et al.* (1977) also show that in children the development of ability to solve this problem is completed only at the age of 4 years.

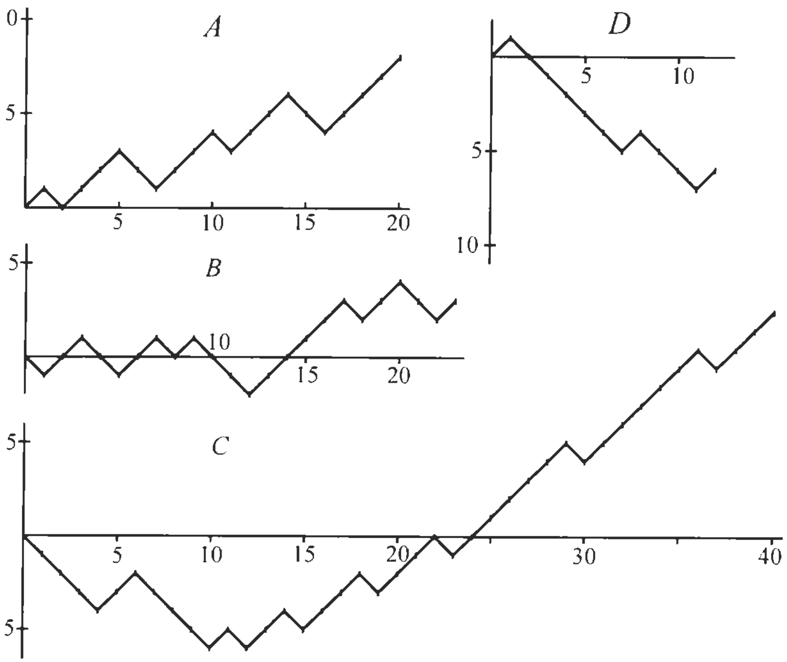

Figure 7. Individual patterns of correct and incorrect choices in dimensionality problem solving by 3-month-old crows (*A–D*). Explanations in the text (see also Figure 1).

4.3 *Dimensionality Problem Solving*

This test was carried out on 29 3-month-old birds and 16 6-month-old birds (Zorina and Krushinsky, 1985, 1987).

During the first trial the choices of voluminous objects by young birds of both groups did not exceed the chance level. Upon repeated trials (in several birds up to 40 trials) their performance continued to be random and was significantly lower than in adult birds (Figure 2*E*). Analysis showed that in most of birds the correct and incorrect solutions alternate in a random fashion (Figure 7 curve *B*). In the course of 10–12 trials (Figure 7 curves *C*, *D*) several birds displayed a preference for a flat object which is quite unusual for adult birds (1 case in 43).

The ability to solve the dimensionality problem in the first trials was revealed in only two birds (Figure 7 curve *A*), whereas two other birds displayed the correct solutions only after a long period of predominantly incorrect solutions (Figure 7 curve *C*). None of the adult birds revealed such patterns.

Analysis of the results of the first five presentation of dimensionality problem is also indicative of the existence of fundamental differences in the behavior of young and adult birds. It was found that both groups of young as well as adult birds did not differ in the number of birds choosing objects in a random order. The young birds displayed a statistically significant predominance of correct solutions in no more than 40% of trials, whereas most adult birds correctly solved the dimensionality problem in 80–100% of cases.

In addition the behavior of young birds revealed large qualitative distinctions which were the most clearly seen in the 3-month-old birds. Their reactions to voluminous objects appeared to be random and without purpose especially in the first trials. In many instances they performed no choices whatsoever ("refusals" as in the extrapolation task). In the course of the first five trials the 3-month-old birds "refused" from solution in a 26%, in contrast to 12% in adult birds ($p < 0.01$).

Estimation of the latency in problem solving showed that, compared to latencies in adult birds, in 3-month-old birds they are nearly 1.5 times as long during the first trial (39.3 + 7.1 s and 23.6 + 4.1 s, $p > 0.05$) as well as during the first five trials (34.5 + 3.4 s and 22.1 + 1.9 s, $p < 0.01$). It is also important that in many instances, the birds while toppling over 3-dimensional objects, seem to be far from waiting for something to be found inside and abandon them almost immediately. A typical behavioral pattern in young birds is to look under the platforms and to try pecking at them, which is very rare in adult birds. In the course of preliminary demonstrations of objects before testing, the 3-month-old birds manipulate them on fewer occasions than do adult birds; i.e. they choose "flat" objects more often, whereas adult birds appear to give preference to voluminous objects.

Thus, our data revealed that the *Corvidae* are unable to solve the dimensionality problem at the age of three months as well as at the age of six months.

In conclusion, it may be inferred that 3-month-old crows are virtually incapable of the studied types of reasoning, despite full development of the basic instinctive (Species-Specific) behavioral patterns indispensable for survival under natural settings (Zorina, 1983, 1989) and the ability for the most complex type of discrimination learning (Zorina *et al.*, 1989). This supports the hypothesis that the processes of learning and reasoning are based on quite distinct mechanisms with different periods of maturation in onthogeny.

4.4 Postnatal Brain Development in Corvidae

The above data indicate that tile reasoning abilities in birds appear only after long-term development in the postnatal ontogeny, thus raising the question about the changes in avian brain structure which take place during this period. This aspect has not been satisfactory studied in any *Corvidae* bird species, because the majority of studies concerned with brain development have been confined to the perinatal period and devoted to precocial avian species.

The initial stage of our analysis of this problem was the investigation of changes in the absolute weight of the avian brain and of some cephalization indices described by Portmann (1946). Our brain studies, conducted in 90 hooded crows (Zorina and Markina, 1987), showed that growth of their brain weight is completed at the age of two months. According to Voronov (1989), this process also continues during the third month of life. During the same period the Portmann index (the ratio of the weight of brain hemispheres to that of the brainstem reaches its maximum value. Thus, as regards the above characters, the crows at the age which is of interest to us do not differ from the adult birds.

A drastically different picture was provided by studies of brain myelination in 3- and 12-month-old birds. It was found that during this period the process of myelination is very intensive and the degree of brain myelination in 3-month-old birds is quite different from that in 12-month-old birds. Consequently, in *Corvidae*, at least during their first year of life, the processes of brain tissue differentiation continue to take place without an increase in brain weight.

This inference is also supported by the developmental studies of the brain cytoarchitectonics in *Corvidae* reported by Voronov (1989). These

Table 9. Distance of natal dispersal in Pied Flycatchers in different parts of its breeding area.

Region	*Numbers of captures*	*Distance between the birthplace and the breeding site (km)*						*References*
		0–1	*1–10*	*10–20*	*20–40*	*> 40*	*> 100*	
Karelia, Russia	43	41.9	46.5	11.6	–	–	–	Artemyev and Golovan, 1983
Estonia	1239	26.6	46.1	14.4	9.4	2.8	0.7	Leivits and Vilbaste, 1990
Latvia	87	50.6	42.5	2.3	1.2	–	3.4	Chaun, 1958
Courish Spit, Russia	258	23.0	68.4	7.0	1.6	–	–	Sokolov, 1991*a*
Oka reserve, Russia	73	37.0	63.0	–	–	–	–	Likhachev, 1955
Dresden, Germany	94	67.0	27.6	3.2	1.1	1.1	–	Creutz, 1955
Gelgoland, Germany	88	71.6	22.7	4.5	1.2	–	–	Likhachev, 1955
NE, Germany	930	50.0	37.5	6.0	4.5	2.0	–	Berndt and Sternberg, 1969

(Sokolov *et al.*, 1987). In the following year, most of the yearlings detected appeared to breed at a distance of 5 km from their natal place. Thus, the birds bred predominantly in the region where they had happened to be upon their juvenile dispersal (Figure 7). In other species with less pronounced postbreeding dispersal, most yearlings initiate breeding within 1 or 2 km of the native nest. A highly pronounced positive correlation is revealed between the postbreeding and natal dispersals in migratory birds on the Courish Spit (Sokolov, 1991*a*). It is commonly assumed that a significant percentage of birds settles within long distances of the area although no reliable data have been reported (Malchevsky, 1968, 1969; Zimin, 1988). However, captures of ringed birds rather confirm a relatively small percentage of birds settling within large distances (Table 9).

At the Courish Spit, the majority of Pied Flycatchers (about 70%) initiate breeding southwest from the natal place (Sokolov *et al.*, 1990). This is caused by the birds' shifting mainly southwest from their birthplace during dispersal. Birds which hatched in those years when breeding was

birds with a high level of reasoning development. It was found that the proportion of crows capable of solving the extrapolation problem was 79% (Krushinsky, 1990); the dimensionality problem – 50%; the test with two voluminous objects – 30%; the Revecz–Krushinsky test, – 36%, albeit mainly in the form of "incomplete solutions". In the contrary, the ability for relative numerousness judgment was found not only in virtually all *Corvidae* but also un pigeons, which supports their earlier described ability of spontaneous integration of isolated elements of previous experiences (Epstein, 1987). In other words, the enlargement of a set of applied tests made it possible to demonstrate that birds such as pigeons, which possess a low level of cognitive ability, are not totally devoid of reasoning, although they are able to solve only a few types of problems.

Let us now consider the extent to which our data answer the four types of questions which, according to Tinbergen (1963), should be answered by behavioral studies.

5.1 Mechanisms Underlying Reasoning in Birds

The mechanisms which underlie reasoning in animals, has not been adequately studied to date. The studies of Krushinsky are an example of the most consistent and fundamental approaches to this problem. The thesis that reasoning is mediated by processing of memorial representations, may be regarded as being commonly accepted (Gardner and Gardner, 1985; Dashevsky, 1977; Firsov, 1972; Ladygina–Kohtz, 1965; Natishvili, 1987; Premack, 1978, 1983; Terrace, 1984). These representations include so called "empirical laws" according to Krushinsky (1990) and consist the part of bird's "cognitive map". Our data support this concept. Despite the diversity of the tests we used to evaluate various aspects of reasoning in birds, their solution requires not an automatic responses to the available stimuli acquired at the expense of previous reinforcements but a decision making based on mental comparison and the immediate combination of information received. In the extrapolation test this is a mental comparison of the directions of movement of the cups, with and without food-bait after their disappearance from the field of view; in the dimensionality test and test with two voluminous objects, this is a mental comparison of the geometrical character of the bait, which is absent at the moment of choice, and those of the available objects; in the Revecz–Krushinsky test this is a comparison based on information on bait locations in at least two preceding trials; in the test of relative numerousness judgment information is processed on the number of reinforcement items previously related to each of the colored stimuli.

Our data also provide new evidence that the processes which underlie reasoning are quite different from those of learning. This is confirmed by drastic differences of all behavioral indices in group G1 birds in solving the dimensionality reasoning problem – which has a logical structure and single-value solution – and those in discrimination control test under conditions of strict comparability of all outer attributes of experimental design and procedure. This is also supported by a specific structure of the experience gained from repetitive dimensionality problem presentations, as well as by the differences in the latencies in various bird groups. Probability analysis of the behavior of birds in solving the Revecz–Krushinsky test also revealed large distinctions from the behavior based on the use of trial and error. Even among the birds which have not met the criterion of problem solving, there was a statistically significant increase in the proportion of birds whose behavior was different from that expected at "random wandering" (Zorina and Salimov, 1989).

The difference of these processes is also indicated by the data on selective effects of the brain lesions in birds (Fedorova and Zorina, 1985; Zinovieva and Zorina, 1976; Zorina and Popova, 1976, Zorina and Fedotova, 1981, Zorina *et al.*, 1982), mammals (Adrianov *et al.*, 1987) and reptiles (Ochinskaya; ref. to Krushinsky, 1990) on their reasoning, and learning abilities. This inference is also supported by the data on large differences in the time of maturation of these processes in ontogeny (Zorina and Krushinsky, 1985, 1987; Zorina *el al.*, 1989).

The use of a set of tests allowed also the analysis of another aspect of the reasoning mechanisms. A number of authors put forward the idea that different types of reasoning are based on different mechanisms (Premack, 1983; Gillan, 1981). The above data on the differences in the extent of successful problem-solving by *Corvidae* also indicates that their solutions are based on processes having their specific features in each case. This is also confirmed by our findings that lesions of the Wulst in *Corvidae* causes a virtual total loss of their extrapolation ability, but does not affect their ability to solve the dimensionality test (Zorina *et al.*, 1982).

As regards the factors controlling the levels of reasoning capacity within the limits of avian class, it has also been established that *Corvidae* differ from pigeons in having a higher specific density of neurons and the number, diversity and complexity of supracellular associations (Voronov, 1989). These data support earlier reports on the importance of relative brain weight, progressive development of phylogenetically young structures of the hyperstriatum and fine differentiation of neurons (See Krushinsky *et al.*, 1982, 1985; Obukhov and Lobanova, 1985).

5.2 *Some Evolutionary considerations*

Our approach, based on the use of various tests, provides valuable data for the comparison of reasoning in birds and mammals. As mentioned above, a single criterion – extrapolation ability – was used as a basis for concluding that the avian class is characterized by the same range of reasoning ability gradations as the mammals (Krushinsky, 1990). According to this viewpoint, the *Corvidae* possess the same level of reasoning capacity as do predatory mammals. The use of the dimensionality test showed that by their ability to solve this problem, the *Corvidae* are superior to predatory mammals and are close to monkeys, dolphins and bears, not only in certain quantitative indices but also in the behavioral strategies employed (Krushinsky *et al.*, 1979, 1982; Zorina, 1982). The use of the Revecz–Krushinsky test and a comparison with the findings reported by Kamil (1988) on the learning - set formation makes it possible to conclude that this similarity is not occasional but reflects the general level of cognitive abilities of Corvidae, which was found to be higher than the respective level seen in predatory mammals and was comparable with that of monkeys. This inference is also confirmed by the studies of the cognitive abilities of parrots conducted for a number of years by Pepperberg (1978–1990).

The above considerations illustrate the hypothesis on parallelism in the evolution of reasoning in birds formulated in the 1960s by Krushinsky (1965, 1990). Apparently, this parallelism relies on common trends of the morphophysiological progression of the forebrain in vertebrates of these two classes (Bogoslovskaya and Zorina, 1986; Bogoslovskaya and Polyakov, 1981; Krushinsky *et al.*, 1985) which is in agreement with Zavarzin's theory of parallel tissue evolution.

At the same time, large differences between the levels of reasoning development in pigeons and crows, whose brains achieve different levels of evolutionary development within the avian class, illustrate the concept of Krushinsky (1990) and some other authors (Warren, 1977; Rumbaugh and Pate, 1984) that in the process of evolution of reasoning increased the number of types of reasoning tests solved by animals.

5.3 *Reasoning Development in Ontogeny*

The data presented in this chapter also make a definite contribution to the virtually unexplored ontogeny of reasoning in birds, as well as to the late postnatal ontogeny of the avian brain which also remains to be fully elucidated. Reasoning abilities have been shown to require a substantially longer period of postnatal development than those needed for learning abilities (Zorina *et al.*, 1989) as well as the innate patterns of social (Zorina, 1975, 1977), exploratory (Zorina, 1983) and manipulatory (Zorina *et al.*, 1986; Deriagina *et al.*, 1983, 1988) behavior in *Corvidae*.

The problem of environmental factors involved in this process requires special investigation; none the less, our data allowed to elucidate the relationships between appearance of reasoning ability and some developmental stages in bird brain ontogeny. It has been established that in *Corvidae* the development of brain weight is completed as early as the third postnatal month (Zorina and Markina, 1987), whereas the process of myelination and formation of large neuroglial complexes continues at least over the entire first year of life (Voronov, 1989).

5.4 *Reasoning Capacities in Birds and their survival Value*

In addition to the availability of virtually all known types of reasoning, the *Corvidae* are also characterized by high levels of simpler forms of higher nervous activity. Their performance in time – based discrimination learning are superior to pigeons (Powell, 1973). Even the patterns of manipulatory activity in crows is rather more complex than in pigeons and seems to be closer to that of the monkeys (Zorina *et al.*, 1986; Deriagina *et al.*, 1983, 1988). These data allow to suggest that high level of Corvidae brain structure determine not only their cognitive abilities but also the peculiarities in species-specific patterns of behavior of *Corvidae* in their natural habitat.

The *Corvidae* are known to occupy the leading place among species with high adaptivity to anthropogenic stresses (Konstantinov and Ilyichev, 1990). Numerous observations and naturalistic studies show that the behavior of these birds is characterized by high plasticity which manifests itself in all behavioral patterns – foraging, playing, exploring, nest-building. It is observed in individual specimens as well as at the level of species, groups and populations. The numerous but uncoordinated and disparate observations of the behavior of *Corvidae* under natural environment reveals their capacity of continual evaluation of environmental changes and appropriate optimal decision making. They are characterized by the absence of stereotypic behavior, even in standard situations. For example, Vakhrushev and Zyuzin (1984) showed that the distance of crow-scaring in town is substantially dependent on the sex, age and behavioral peculiarities of the approaching human, because the crows assess each situation as a new one, analyze it and use it as basis for decision making.

The studies reported by Zach and Smith (1981) provide evidence that such a seemingly stereotypic behavioral pattern as breaking shells to feed on mollusks reaches a close-to-maximal efficiency level in Northwestern crows. It was found that the studied population of crows drop whelks only on hard rocks, choose larger whelks which are easier to break and fly up to the height, necessary and sufficient for the shells to break impact. If a shell is not crushed in the first attempt they repeat it, which is energetically more advantageous than flying to fetch another shell. On the contrary, in the same situation herring gulls displayed stereotypic behavioral patterns (Tinbergen, 1963).

It is commonly accepted that one of the major manifestations of reasoning in animals is their tool-using behavior. Some examples have been described in which individual *Corvidae* have assessed a particular situation and the used tools to solve this specific problem. According Jones and Kamil (1973), a jay, deprived of food before the experiment, tore off and bent strips of newspaper spread on the cage floor and used these to rake up small pieces of food scattered outside the cage previously out of its beak reach. Similar observations were reported by Fabri (1970), Powell and Kelly (1975), Gayou (1982) and Reid (1982).

Thus, experimental data on reasoning ability in *Corvidae* may be used as a basis for the physiological interpretation of their behavior in the wild (Zorina, 1984).

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INDEX

(Continued from the inside front cover)

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