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Experimental investigations on the behavioural differences between urban and forest Blackbirds

Badania eksperymentalne nad zróżnicowaniem zachowań kosów populacji miejskiej i leśnej

Abstract. A series of ethological experiments have been carried out on forest and urban Blackbirds reared in identical laboratory conditions. During the first year of their life migratory restlessness was studied on the forest and urban population. The tests: open-field, tonic immobility, handling and predator presentation have been conducted. Urban Blackbirds did not differ from the forest ones in exhibited migratory restlessness. The results of the remaining experiments show that urban Blackbirds adapt more rapidly to experimental situations. The birds of both populations congenitively recognize the function of mobbing calls, but these constitute for them a signal to different behaviour. Urban Blackbirds respond with mobbing while forest ones exhibit the tendency to hide. This difference is connected with the existence of different selective pressures in the two environments.

CONTENTS

I. INTRODUCTION

Urbanized populations of the Blackbird were recorded for the first time from Western Europe more than a hundred years ago (HEYDER 1956, STEPHAN 1985), A spreading of urbanized populations is presently observed (LUNIAK, MULSOW 1988). A number of ethological differences were observed between the urban and the forest populations. Most controversial is the problem of the emergence of new urban populations: are they the result of colonization of new towns by birds from urbanized populations, or do they appear independently in various localities? This is connected with the question whether changes observed in the behaviour of urban birds are due to adaptation of adult individuals or occur in ontogenetic development, or if they are hereditary. The aim of the study was to investigate the mentioned problems.

Reported ethological adaptations of Blackbirds of urban populations to life conditions in an urbanized environment have included a reduced escape distance from man, i.e. one to several metres, as compared with the distance in forest ones, 60—80 m (Graczyk 1963), and the prolongation of daily activity (feeding and singing) into evening or even night hours due to artificial lightening of towns (Mitchell 1967, Oertel 1979).

It is the former feature that proves to be the most profitable. Birds diminishing their escape distance thus obtain protection from predators, whose escape distance from man is always superior to that of the Blackbird. It has been shown that breeding success in nests in the vicinity of man's constant presence, or on buildings, exceeds that in birds nesting further away (Osborne, Osborne 1980).

The present work assumed that the emergence of an urban population resulted from complex selective pressures of ecological and ethological character, the main factors of the latter pressure being (1) the constant presence of man, forcing the decrease of escape distance in individuals inhabiting urban areas, and (2) the variability of urban environment conditions resulting from human activity; the changes are much more frequent and more significant than is the case in forest environment. This variability of environment in towns can be treated as a great heterogeneity and changeability in visual and acoustic stimuli.

The mentioned factors make the urban environment much richer in stimuli, so that birds should rapidly distinguish changes in their environment, rapidly respond to them, and adapt rapidly to a new situation unless it threatens their lives.

It is only the experiments in ethology on birds reared since their nestling age and taken when the cognition of urban or forest environment was still impossible that can yield data for stating the acquired or hereditary character of the observed features.

It has been assumed while planning the ethological tests that they should aim at the recognition of such behaviour as might be of adaptive importance in the specific urban conditions. However, laboratory conditions cause limitations as to the kind and scope of realizable experiments. Such tests, according to some previous assumptions, should yield the response of the animal to a novel environment (experimental conditions), and the reaction to direct threat by predator, as well as measure the reaction speed to the exposition of a given stimulus, the response intensity to a given stimulus, and the variations in the intensity and speed of response in repetitions of the experimental procedure.

The experiments also aimed at determining whether qualitative differences would occur between behaviour of individuals of the compared forest and urban populations.

Research was also conducted on the appearance of migratory restlessness treated here as a behaviour showing the distance covered by migrating birds. This study was carried out in the first autumn and spring of the Blackbirds' life.

The following ethological tests were conducted during the second and third year of each Blackbird's life: (1) studies of behaviour in open-field test, (2) experiments with tonic immobility, (3) reaction to handling, and (4) research on behaviour in reaction to predator presentation.

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II. MATERIAL AND GENERAL METHODS

Blackbirds *Turdus merula* LINNAEUS, 1758, were used in the experiments. They were taken from nests of urban and forest populations and subsequently reared in identical laboratory conditions. The forest Blackbirds were from forests seldom frequented by man in various parts of Poland. All such forests were situated at least a dozen or so kilometres from towns. The urban birds were taken in Cracow, Poland, from places characteristic for constant human presence there, i.e. the town parks. The experiments were carried out on birds originating from four broods of forest Blackbirds (3 males and 7 females) and from four broods of urban birds (8 males and 7 females).

The nestlings were taken from nests at the age of 7—10 days. They were transported to the laboratory in darkened containers. All birds in rearing were individually marked with coloured rings. Nestlings of the same brood were kept together up to the moment of their acquiring the ability to feed on their own. Older nestlings were moved to individual 44 ×60 ×47 cm cages opened only during feeding.

Younger nestlings were initially fed each 30 min. with the frequency of feeding being diminished in the later days. Older ones were also left food in their cages so that they might try feeding between feeding times. This was also enhanced by the prolongation of intervals between feeding periods. At the age of 15—19 days, all nestlings were taking food from containers on their own. They were then moved to rooms where they remained in individual cages during the whole length of the experiments. Adult birds were fed with the standard mixture containing boiled hen eggs, wheat bran, cottage cheese, carrot, and horsemeat.

The following measures were undertaken in order to preserve identical rearing conditions and to minimize disturbing the birds:
— urban and forest birds were kept in the same rooms, yet all cages were separated with opaque partitions so that a bird could hear but not see others;
— the rooms' windows were covered with granulated foil, which was translucent yet did not make it possible to see objects outside;
— rooms had the natural yearly lightening rhythm (no artificial light was used);
— containers with food were changed once per day between 9:15 and 9:45;
— the rooms with birds were accessible to the person exchanging containers with food and water (solely during feeding) and the experimenter only;
— any person entering the rooms for exchanging food, cleaning or other activities not connected with capturing birds was clothed in a lab white apron;
— in all situations connected with capturing birds, i.e. for experiments, weighing, moving to another cage, etc., the person performing such tasks was always clothed in a black apron. Those conventions were to minimize the stress connected with human presence and to standardize the conditions of rearing activities;
— in order to control the general condition of the birds, they were weighed on average once per month and each time they were taken for experiments or moved to other cages. The bottom of all cages was covered with sand, on which the daily-exchanged container with food and water was put. Each cage was equipped with two wooden perches for the birds to rest on. No action for taming the Blackbirds was undertaken, so none of the reared birds exhibited any signs of taming.

All experiments were carried out by the same one experimenter. The same clothes were used all the time: trousers, shirt, shoes and black apron. The sequence of experiments with a particular bird was established separately for each series with a random numbers table and the results were worked out after a whole experimental series had been carried out. Such proceedings were to unity the experimental procedure and eliminate the role of suggestion in conducted observations and ethological experiments.

The statistical significance of differences recorded in the particular experiments within both groups was examined with Wilcoxon paired-sample test and the significance of differences between experimental groups was studied with Mann-Whitney U-test (Zar 1974). The significance level limit was settled at 0.05 for the two-tailed test.

III. MIGRATORY RESTLESSNESS

1. Assumptions and methods

Studies by Berthold (1973, 1975, 1978, 1984) show that migratory restlessness reflects migratory activity, and the duration and intensity of this restlessness corresponds to the distance covered by a migrating individual; the appearance of passage periods in the yearly cycle is controlled by endogenous factors and the tendency to migration is hereditary.

This permits to formulate the hypothesis that urban Blackbirds should exhibit, a significantly shorter duration of migratory restlessness than those of forest populations. Also, the intensity of migratory restlessness in urban birds should be much lower.

The Blackbird is a night migrant. It would be then sufficient to record the night activity of the birds for obtaining an image of its intensity (number of movements per time unit) and the duration of the migration period (number of days).

Research was carried out in special cages for individual recording of 24-hour' activity. Each movement of a bird was represented by an electric impulse transmitted to the recorder's memory. This system permitted the simultaneous recording of impulses from 10 cages. All experimental series lasted 2—3 weeks. After that time other birds were put into cages. Each time the same number of urban and forest birds were studied. The aim of this procedure was to investigate all birds during the autumn or spring seasons.

Data of October/November and March/April of each bird's first year of life were analysed. A bird was assumed to exhibit migratory restlessness in a given day if between 23 and 03 hrs at least five 5-minute intervals were recorded, during each of which the bird made at least 4 movements. The results were presented as (1) the number of birds exhibiting migratory restlessness, (2) mean number of 5-min intervals with migratory restlessness per day of study in each individual calculated as the ratio of the number of 5-min intervals with migratory restlessness to the number of days in which this restlessness was studied, and (3) mean number of movements per interval with migratory restlessness in each individual calculated as the ratio of total movements in all 5-min intervals with migratory restlessness to the number of those intervals.

2. Results and discussion

During the first autumn of life, 15 individuals of the urban and 10 individuals from the forest populations were studied (Table I). Migratory restlessness was recorded in 7 urban and 7 forest birds (Table I). Mean number of 5-min intervals with migratory restlessness was 1.04 and 0.99 in urban and forest Blackbirds, respectively. The intensity of migratory restlessness was on the average, 26.5 and 22.8 movements per one 5-min interval with migratory restlessness in urban and forest birds, respectively (Table II). The differences between the mean values are of no statistic significance.

Table I

Comparison of numbers of urban and forest Blackbirds with observed migratory restlessness

Life period	Total birds number		Migratory restlessness		Statistic significance (series test) $p < 0.05$
	urban	forest	urban	forest	
1st autumn	15	10	7	7	NS
1st spring	10	10	7	6	NS

Table II

Intensity of migratory restlessness in urban and forest Blackbirds. Comparison of results obtained in experiments for migratory restlesness in urban and forest Blackbirds. All differences of no statistic significance

Life period	Amount of migratory restlessness	Urban birds	Forest birds
1st autumn	mean number of 5-min intervals with restlessness per bird per day of studying	1.04	0.99
	mean number of movement per interval with restlessness	26.50	22.80
1st spring	mean number of 5-min intervals with restlessness per bird per day of studying	5.83	7.96
	mean number of movement per interval with restlessness	207.50	287.70

During the first spring of life, 10 individuals of the urban and 10 individuals of the forest population were studied. Seven urban and six forest birds exhibited migratory restlessness (Table I). This restlessness was much more intensive in spring than in autumn. A similar regularity has already been reported in the Blackbrid (Bąkowska 1965) and in other species of birds (Preston 1966). This is explained by the fact that the autumn migration is extended in time and passage usually is of low intensity, while that in spring is much shorter and much more intensive (Berthold, Gwinner 1971, Preston 1966).

Mean values for urban birds were, respectively, 5.83 (number of 5-min intervals with restlessness) and 207.50 (mean number of movements per one 5-min intervals with restlessness); they reached respectively 7.96 and 287.70 in forest birds. Although the obtained values do not differ statistically, it should be stated that the highest values occurred in the forest group; this would suggest a stronger tendency to migration within this group.

Considerable individual variations of the occurrence and intensity of migratory restlessness have been recorded in both groups. Similar differences have also been reported in other species (GWINNER 1968, 1972). It has been established that such important variations in migratory restlessness are exhibited by the species which contain both migrating and non-migrating populations (GWINNER 1972).

The results obtained (Table II) show that at least in the first year of life, the Blackbirds of the urban population do not differ significantly from those of the forest in their tendency to migration. This is supported by SCHWABL'S (1983) research who noted that the majority of Blackbirds of urban populations migrate in the first year of life. Studies consisting in crossbreeding, in various combinations, the individuals of migrating and non-migrating population of the Blackcap (BERTHOLD, QUERNER 1982) and of the Robin (BIEBACH, 1983) show that the tendency to exhibit migratory restlessness has genetic grounds.

It becomes clear, then, that the selection does not tend to eliminate tendency to migration from the population of sedentary birds, at least in the case of one-year-olds. A wintering population faces the danger of extinction if confronted by particularly difficult winter conditions (DOBINSON, RICHARDS 1964, HAARTMAN 1968). This is supported by results of investigation of the Stonechat *Saxicola torquata* (DHONT 1983) and of the Blackbird (SCHWABL 1983, KARLSSON, KALLANDER 1977, KALLANDER, KARLSSON 1981), which stated that winters significantly reduce the population of wintering birds. After such winters, the breeding population is much smaller, contains a higher percentage of migrants and is restored with migrating individuals.

IV. THE OPEN-FIELD TEST

1. Assumptions and methods

The open-field test is commonly used in studies on emotionality, fear and response to novelty in animals (HALL 1934, ARCHER 1973). So far, however, the test has been used only for laboratory animals such as rats (RUSSEL, WILLIAMS 1973, GRAY, LALLJEE 1974), mice (GRAY, CONNEY 1982, POWELL, WOLFF 1982) guinea pigs (SUAREZ, GALLUP 1982) and ducklings and chicks (MURPHY 1978, FAURE et al. 1983). No adult wild animals have been studied so far, so a number of tentative experiments had to be carried out before initiating the present study in order to establish the experimental procedure.

The adaptation of the test to the needs of the present work was based on the assumption that it should yield possible differences in response to novel, experimental situations and the occurrence of anti-predator behaviour (GALLUP, SUAREZ 1980, SUAREZ, GALLUP 1980).

The experiment used a circular arena with a diameter of 1 m, surrounded by 50 cm walls. The floor and the wall of the arena were painted white. A container with food and water was placed in its centre. A TP—K 16 TV camera was placed 120 cm above the centre of the arena. The space between the camera lens and the walls was covered with white canvas to prevent the bird in the arena from seeing anything outside. A microphone was placed near the camera. Equipment for observation of the experiment was placed in an adjoining room. The arena was lit with three 150 W bulbs 155 cm above the arena's floor. In order to unify the conditions of placing birds in the arena, a special box was used, equipped with a piston. A rectangular opening was made in the wall of the arena; it could be covered with a white barrier. Each bird was taken out of the canvas bag in which it was brought from the rearing room and placed into the box. The box was then put by the opening in the wall of the arena and the piston was used to push the bird out of the box and into the arena. The opening in the wall was then closed.

The birds were brought into experiment rooms, which were obscured all the time. Only a small lamp was used to enable movement in the rooms. The bird's behaviour was observed on a TV screen. The view of the arena on the screen was divided into sectors. The birds' calls during the experiment were recorded on tape. During the experiment, the latency time was noted until the first movement of the head — L1, of the whole body — L2; ambulations, head movements, time of full immobility, number of vocalizations by the birds and the number of approaches to food and water were also registered. After the experiment, the number of defecations in the arena and in the box were counted. The arena was cleaned after each experiment. The experiments were conducted in the morning hours 09—12. The birds' containers with food and water were exchanged in the cages only after the experiment.

The experiment lasted for 10 min. The behaviour of the birds was noted in 10-sec. intervals. This mode of recording in such experiments was earlier used by Hogan and Degabriele (1982). All enumerated types of behaviours appearing during that time were registered. After the experiment a control hearing of the recorded tape was done. Time was measured with a tape with recorded counting from 1 to 60 in 10-sec. intervals, corresponding to the numbers of the intervals. The lighting of the arena was gradually (so as not to cause a lighting shock) turned on by means of an autotransformer on receiving a signal from the recorder. The counting on the tape began when the arena was fully lit. After the end of the experiment, the bird was captured with a small net, the arena cleaned, and the next bird was put into the arena. The experiment was conducted thrice with each bird on three consecutive days. The experiments were marked with Roman numerals (I, II, III).

2. Results and discussion

The reaction pattern of the Blackbirds in the open-field test was as follows. Most frequently the bird pushed into the arena did not move at all for, on the average, the first 4 min. After that time it began to move its head, to

„look around", to examine closely its surroundings. After 7—8 min, the bird moved on, it began to walk, slowly and stopping at first, later regularly penetrating the floor of the arena. 0 to 4 defecations took place during the experiment, on the average 1.27 and 1.00 for urban and forest birds respectively (Table III).

Table III

Results of the open-field test in urban and forest Blackbirds. Compared mean number of activity occurrences and mean numbers of 10-sec. intervals with particular behaviours. All differences of no statistic significance

Measurement mode	Behaviour	Three (I-III) experiments mean value for whole group	
		urban birds	forest bird
Mean number of activities	defecations	1.27	1.00
	number of sectors crossed	12.73	29.52
Mean number of 10 sec. intervals	— until first head movement (L1)	23.15	23.07
	— until first body movement (L2)	43.79	48.30
	— of total immobility	33.18	35.81
	— during which the bird moved its head (surroundings surveillance)	26.79	24.19
	— with walking	8.55	7.62
	— with alarm calls	0.54	0.22

A considerable individual variation was noted in the behaviour of the two groups. Latency time until the first head movement was from 0 (one case) to 60 10-sec. intervals (10 min) — i.e. the bird did not move at all. The mean values for urban birds and those of the forest were, respectively, 23.15 and 23.07 time intervals (Table III). Latency time until first body movement was from 6 to 60 10-sec. intervals (the bird did not move until the end of the experiment). The mean values for urban and forest birds were similar 43.79 and 48.30 respectively (Table III). Head movements occurred, on the average, in 26.79 time intervals in urban Blackbirds and in 24.19 intervals in forest ones, the extreme values being 0 and 58 (Table III). The other behaviours were expressed only by some of the individuals. Distress-calls were made by 5 urban birds and only 2 forest ones. One urban and 2 forest birds used food. A similar situation was in the case of water. None of the urban birds attempted flight in the arena, while four birds of the forest group tried it. Four birds in each group moved enough to change sectors. Others just turned in circles or did not leave the sector in which they had been placed. The discrepancy in the mean number of sectors crossed between urban (12.73) and forest (29.52) birds is due to an exceptionally intensive activity of a forest male.

All differences between the groups are statistically non-significant. The analysis of changes in response in expt. I—III within each group revealed differences in time of active observation of the surroundings in females (head movement) (Table IV). In urban females, the time devoted to head movement was high in expts I and II and significantly decreased in III ($p < 0.05$). The decrease of the time devoted to the active observation of the surroundings in urban females during expt. III shows that the birds got to know the surroundings enough to prevent further observation from feeding them more new information. On the contrary, in forest females the time of head movement significantly decreased in expt. II. In expt. III this time significantly increased ($p < 0.05$). The decrease in expt. II proves that those birds reacted more strongly to the repetition of the experiment in expt. II; for latency times L1 and L2 are the highest in the second experiment while the time devoted to the observation of the surroundings is the shortest. It is only during the third experiment that forest females spent more time at getting to know their environment.

Table IV

Mean number of 10-sec. intervals with head movements (surroundings surveillance) in urban and forest Blackbird females in particular experiments of the open-field test

Experiment	Urban Blackbirds	Forest Blackbirds
I	29.71	20.43
		*
II	27.71	9.86
	*	*
III	20.00	27.72

* Asterisk marks differences statistically significant at the level of $p = 0.05$

V. TONIC IMMOBILITY

1. Assumptions and methods

Tonic immobility, also known as animal hypnosis, occur in nature as the reaction of an animal directly threatened by a predator (Gallup et al. 1971, McFarland 1981, Sargent, Eberhardt 1975, Thompson et al. 1981). It is manifested in the tonic immobility of the whole body. Laboratory research on rabbits and chicks have showed that various factors decrease or increase the duration of catalepsy (Gilman et al. 1950, Ratner, Thompson 1960, Salzen 1963, Hughes 1979, Arduino, Gould 1983). It has also been shown that the capability to enter into tonic immobility is hereditary: races of rats (McGraw, Klemm 1973) and chicks (Gallup 1974) have been selected according to low and high capability to enter catalepsy.

Assuming that urban Blackbirds are innately characteristic by the ability to quicker adaptation, it should be anticipated that the catalepsy time in the second (i.e. repeated) experiment will decrease at a higher rate than in the birds of the forest group.

The experiments were conducted twice with each bird in a one-week interval. They were carried out in the morning before exchanging containers with food and water in rearing cages. The birds were transported in canvas bags and placed in a darkened experimental room. Foam polystyrene walls covered with canvas were placed on the experiment table so that each bird had the same field of vision. The place of the experiment was lit with a 60 W bulb pointed at the ceiling of the room. Time was measured as described in Sec. IV, 1. A bird taken out from the bag was immobilized against the table lying on its left side. After 15 secs the experimenter withdrew his hands. The experiment ended when the bird stood up.

2. Results and discussion

In the first experiment, the urban Blackbirds had their mean time of tonic immobility much longer than that of the forest ones (319 and 130 secs, respectively); such discrepancy is statistically significant ($p < 0.02$) (Table V). In the second experiment, the mean catalepsy time of urban birds dropped by half to 141 secs, while that of the forest ones remained roughly at the level of the first experiment — 123 secs. The differences yielded by the second experiment are statistically insignificant (Table V).

Table V

Mean duration of tonic immobility in urban and forest Blackbirds (in secs)

	Urban birds	Forest birds	Statistic significance
Experiment I	319.1	130.0	$p < 0.02$
Experiment II	140.9	123.3	NS
Statistic significance	$p < 0.005$	NS	

The results obtained show a greater reactivity of urban Blackbirds evidenced by the longer immobility time in the first experiment. The shortening of this time in the second experiment shows their capability to rapid adaptation to the experimental procedure. The forest Blackbirds had a similar tonic immobility time in both experiments, what would suggest a more rigid reaction pattern. As the two groups of birds were reared in identical conditions, the results obtained point to the hereditary character of the recorded differences.

The results obtained show that urban Blackbirds react much stronger to a novel situation as they are quicker in adapting to the repetition of an experimental situation. This is of importance in an urban environment, where the feeding and nesting places of the Blackbirds may undergo rapid and unexpected changes. The more rigid reaction pattern exhibited by the forest Blackbirds is connected with the greater stability of forest environment.

VI. HANDLING TEST

1. Assumptions and methods

The term handling is commonly used in ethological literature to denote any human manipulation of experimental animals (Jones, Faure 1981). This occurs in the event of direct contact of man with the animal when it is taken in hands by the experimenter while being moved out of the cage, transported, or put into experimental apparatus.

The handling term occurs most widely in studies on calls emission by birds (Drives, Humphries 1969) and in experiments with tonic immobility (Gilmann et al. 1950). Ornithologists netting birds have already noticed a long time ago that some captured birds emitted calls during taking out from the net while others remained silent (Norris, Stamm 1965). Such behaviour of birds is only observed in nature when a bird is captured by a predator. Distress calls, as contrasted with alarm calls and mobbing calls, are emitted only in the event of ultimate threat to the bird, i.e. when it is caught by a predator (Klump, Shalter 1984). In such a situation a bird might also attempt to peck at its predator (Norris, Stamm 1965). Little is know about the essence of this reaction. It is maintained that the ability to emit distress calls constitutes a conservative behavioural character and a relatively simple, well-defined, innate reaction mode unmodified by learning (Norris, Stamm 1965). A number of experiments was conducted on the frequency of distress calls emission by wild birds (Balph 1977, Perrone 1980, Inglis et al. 1982, Greig-Smith 1982, 1984, Hogstedt 1983). They have shown that the same percentage of individuals always emit distress calls in a given species. Numerous hypotheses tried to explain the role of distress calls (Drives, Humphries 1969, Norris, Stamm 1965, Perone 1980, Hogstedt 1983). However, experimental evidence has so far supported only the hypothesis that distress calls constitute signals for help (Stefański, Falls 1972 a, b) and that the prey's calls serve to attract other predators which eventually might attack the predator holding the prey, giving the latter a chance of escape (Perone 1980).

The present experiment aimed at studying the Blackbirds reaction to handling procedures and multiple repetitions of the procedures during one year.

A standard procedure of taking of the cage, holding in the hand and putting back into cage was constructed. This is of greatest importance, as it has been established before (PERONE, PAULSON 1979) that two experimenters might obtain discrepant results during handling caused by differences in the mode of conducting the experiment. This all experiments were here carried out by the same person at the same time of day between 09 and 11 hrs. Particular attention has been paid to ensure that the course of the experimental procedure be identical in each case. The birds have been accustomed to the procedure since much earlier; after acquiring the ability of independent feeding they were weighed on the average once per month for control of their state of health. Data from the second year of life of the birds were taken into account in results analysis. Each time the behaviour of the bird was noted during holding in hand, after removal from cage, before weighing, and during holding in hand after weighing.

The detailed course of the experimental procedure was as follows:

1. the experimenter entered the room and readied the electric balance, trying to avoid sudden movements;
2. the experimenter approached the chosen cage and captured the bird with a small net, thus shortening the duration of capture;
3. the captured bird was taken out of the net with the right hand and placed in the left hand in the way that its head was situated between the index and the middle finger and the hand held the whole body of the bird, the bird's feet resting on the hand and this immobilized with only slight movements of the head possible;
4. the bird was taken to the place where the balance was situated, the experimenter always facing the balance and with his back to the row of the cages, holding the bird in front of himself in the way that no other bird might see the course of the experiment;
5. the index of the right hand was approached to the bird's beak in order to provoke pecking, three movements of the finger were made in the direction of the beak, the bird's behaviour was noted;
6. the bird's head was freed by withdrawing the index finger of the left hand and that of the right one was moved as above, the bird's reaction was noted;
7. the bird was put into the weighing box, the weight was read and noted, the bird was taken out of the box with the left hand and seized as after removing from the cage;
8. a procedure identical to the one described in 5—7 was conducted;
9. the bird was put back into the cage and a next one was captured.

The following behaviours were distinguished:

Bc — beak closed;
Bo — beak open;
Bp — the bird pecks the experimenter's hand;
Ac — the bird emits alarm calls;
Dc — the birds emits distress calls.

11 to 14 experiments were conducted with each bird, one per month on average. 12 urban and 9 forest birds were used. A total of 160 experiments on urban birds and of 113 in forest ones was carried out.

Mean values form all experiments for each action were calculated for each individual separately for the two differentiated stages (I — before, and II — after weighing the bird), and for the whole series of experiments.

2. Results and discussion

The actions recorded during handling had a very differentiated frequency. Pecking — Bp — occurred most often, the mean values being 2.14 and 2.21 for urban and forest birds, respectively (Table VI). Frequency of pecking was similar in the parts I and II of the experiments. No statistically significant differences were reported between the groups.

Table VI

Comparison of results in handling experiments with urban and forest Blackbirds. Roman numerals I and II denote experiment parts. * — $p < 0.001$

Action	Urban birds	Forest birds	Statistic significance
Beak open Bo I	0,78 *	0.42	NS
Bo II	1.00	0.51	NS
Bo I + Bo II	1.78	0.94	$p < 0.02$
Alarm calls Ac I	0.14	0.07	NS
Ac II	0.08	0.09	NS
Ac I + Ac II	0.23	0.16	NS
Distress calls Dc I	0.10	0.35	NS
Dc II	0.04	0.27	NS
Dc I + Dc II	0.14	0.62	$p < 0.001$
Pecking Bp I	1.05	1.14	NS
Bp II	1.09	1.07	NS
Bp I + Bp II	2.14	2.21	NS
Bo I + Bo II	1.78	0.94	$p < 0.02$
Beak open after return to cage	3.24	2.76	NS
Statistic significance	$p < 0.001$	$p < 0.005$	

The action beak open — Bo — was more frequent in urban birds (mean value 1.78) than in forest ones (0.94). These differences are statistically significant ($p < 0.02$) (Table VI). In the second part of the experiments, urban Blackbirds increased the frequency of opening beaks: BoI = 0.78, BoII = 1.00 ($p < 0.001$) (Table VI). The differences recorded in forest Blackbirds: BoI — 0.42 and BoII — 0.51 are statistically non-significant. The frequency of emitting alarm calls — Ac was very slight in both groups: urban birds —

0,23, forest birds — 0.16, all differences being statistically nonsignificant. The frequency of emitting distress calls was very low in urban birds — mean Dc = 0.14. It was the action with the lowest frequency. On the other hand, the same frequency was relatively high in forest Blackbirds — Dc — 0.62. This value is statistically different from that in urban birds ($p < 0.001$).

During handling, Blackbirds undergo severe physiological stimulation manifest e.g. in the opening of the beak. However, the expression of this behaviour is inhibited during holding the bird in the hand. This is evidenced by the fact of considerable (statistically significant) increase in frequency of opening the beak after putting the bird away back into the cage, and by the observation that the bird returned to the cage had its beak open after the experiment yet closed it immediately after the experimenter's sudden approach to the cage. During handling, however, the inhibition of expression of such behaviour is much stronger in forest Blackbirds (Table VI). The frequency of beak opening was high in urban Blackbirds during handling and increased by 80 per cent after putting back to the cage ($p < 0.001$), being significantly lower in forest birds and increasing by 200 per cent ($p < 0.005$) after return to cage (Table VI).

The frequency of beak opening in urban Blackbirds after return to cage was closer to the maximum. BoII (after return) reached 3.24 (max. 4.0) while attaining only 2.76 in forest birds. Also, the frequency of emitting destress calls was more than four times higher in forest than in urban birds. Distress calls are characterized by the highest threshold value needed to trigger such a reaction. Blackbirds use them solely in the situation of direct threat of capture by predator. The higher frequency of emitting distress calls in forest birds proves that handling, in spite of previous numerous repetitions, still triggered the strongest reaction in those birds. The same procedure causes a much weaker reaction in urban Blackbirds and the inhibition of reaction intensity becomes already visible during handling, as evidenced by the fact of statistically significant increase in beak opening frequency in urban Blackbirds in the second part of the experiment ($p < 0.001$). The fact that the reaction is weaker in urban birds is also proved by the significantly lower frequency of emitting distress calls by those birds. All the above shows that urban Blackbirds were much better adapted to the experimental situation and did not react to it as strongly as the forest ones.

VII. PREDATOR PRESENTATION TEST

1. Assumptions and methods

Research on the reaction of birds to predator presence was conducted in field (Altman 1956, Shalter 1978a, Conover 1979, Conover, Perito 1981, Elliot 1984, Brown 1985, De Laet 1985, Hill 1986) and laboratory conditions (Curio et al. 1978, Shalter 1978b, Jones 1980, Frankenberg 1982, Inglis et al. 1983). Responses to the presentation of the predator were described for various species. Attempts were also made at discovering the causes and mechanisms of such reactions (Andrew 1961 a, b, c, Curio 1975, 1980, 1985, Shalter 1978a, b, Klump, Curio 1983, Shields 1984, Regelmann, Curio 1986).

The reaction to predator presentation test was prepared with the goal of studying the behaviour of the birds of the two groups when confronted with various experimental situations connected with the presentation of novel objects or such that may trigger antipredator reactions. The experimental procedure was constructed so as to enable the series of experiments conducted to disclose the course of such ethological processes as adaptation to constant stimulus presentation, learning of dangerous object, recognition or adaptation to experimental conditions.

Assuming that urban Blackbirds are better adapted to changing conditions, there should be expected a more rapid adaptation to the experimental situation and a greater differentiation of responses to particular stimulus situations.

This test studied the bird's reaction to the presentation of a stuffed Tawny Owl *Strix aluco*. Individuals of this species are natural enemies of the Blackbird in both urban and forest environments (Laursen 1981, März 1954). This is also confirmed by the facts of mobbing an exhibited Tawny Owl dummy by by Blackirds in forest and an urban park (pers. observations).

The experimental cage had the dimensions 75 ×95 ×80 cm. It was placed in a room painted white. A white wooden box for the presentation of the Tawny Owl dummy was placed on the right of the cage. It had the dimensions 25 × ×24 ×48 cm. The rotating movement of the box around its vertical axis was done with use of a remote-controlled electric motor. In its off position, the box's inside faced the outside of the cage so that the bird could not see its content. Each experiment began with a 180° turn of the box so that the bird might see its inside. The operation of taking the owl in and out was unseen by the caged bird. During those tasks the birds exhibited little or no reaction. Two perches were placed in the cage. The perch closer to the rotating box was situated at 55 cm above the cage floor. The more distant perch was at 62 cm above the floor. The perches were connected to an electric system and registering aparatus for recording each use of the perches by birds on tape in the way enabling an easy count of how many times each bird alighted on the closer or the more distant perch.

During the experiment, another tape recorded all vocalizations of the bird, those being heard, at the same time, in the experimenter's headphones. Time was measured with the same device as described in the open-field test.

The experimental procedure was constructed similarly according to Curio et al. (1978). Each experiment consisted of two parts. The first one (minutes 1—5) constituted the proper part of the experiment, during which a given stimulus was presented. The next five minutes (6—10) were devoted to recording the bird's behaviour after response in order to compare its reaction with the experimental part. The beginning of part one was signalled by the movement of the box. Part two began with the backwards movement of the box to the initial position.

The course of the experiment was as follows:

The bird was put into the experiment cage on the eve of experiment I. It was left its food dish taken from its cage and a new water container. The two containers were exchanged at 9:15 a.m. during the three consecutive days of the experiments.

day 1:
7:30—7:40 experiment I with empty box
day 2:
7:30—7:40 experiment II with empty box
day 3:
7:30—7:40 experiment III with empty box

The experiments I through III were then "zero" trials for a novel object presentation, i.e. the white box rotating at 180° at the beginning and end of each experiment and exposing its inside during five minutes (min 1—5). These trials were to give information on response strength to a novel object and on the course of adaptation to a novel object.

8:00 — Tawny Owl dummy placed into the rotating box
8:40 — 8:50 — experiment IV: presentation of the dummy

This experiment was to solve the problem whether reaction to the novelty of the owl would significantly differ from that to the empty box presented in experiment I—III.

10:00—10:10 — experiment V — owl presentation combined with the playback of "tix" mobbing calls of Blackbirds at a rate ca 120—150/min. This tape was prepared by multiplying a 1.5 min recording of one Blackbird mobbing a stuffed Tawny Owl. This experiment aimed at teaching the Blackbirds used in the experiment that the owl is danger object. Curio et al. (1978) have demonstrated experimentally that wild Blackbirds might use mobbing calls to teach other individuals of their species to mob objects dangerous for them by means of cultural transmission. It has been shown that mobbing calls themselves, even without visual reinforcement, when played form tape can transmit the identical information with the one transmitted by live Blackbirds during mobbing reaction (Vieth et al. 1980).

12:00—12:10 — experiment VI — owl presentation without mobbing calls playback.

12:50—12:55 — experiment VII, part 1 — owl presentation as in expt. VI.

Expts VI and VII were the test for learning owl recognition as a dangerous object. They are also to check if the Blackbirds' response to the Tawny Owl dummy would change after playback of mobbing calls in expt. V. and whether the Blackbirds unacquainted with those mobbing calls function from the field can be taught to recognize a danger object in the stuffed owl by those mobbing calls played back from tape. The procedure of those experiments did not differ in any respect from that in expt. IV.

12:55 — 13:00 — experiment VII, part 2 (min 6—10)
min 6 — owl presentation combined with mobbing calls playback
min 7 — owl presentation without mobbing calls playback; at the end of this minute, return of box with owl to initial position
min 8—9 — observation of the bird after return of box (after response situation)
min 10 — mobbing calls playback without owl presentation

An hour after the end of the experiments, the bird was put back into rearing room and the cage was prepared for the next individual.

Part 2 of expt. VII was a repetitions of all situations occurring in the preceding experiments, with the exception of min 10, when the reaction of the birds to only mobbing calls playback was studied without any combination with any additional visual stimulus presentation.

The analysis of the Blackbird's behaviour in min 6—10 of expt. VII was to answer the following questions:

1. Would an individual's reaction strength caused by a particular stimulus situation undergo any change soon after the change of the stimulus situation, i.e. after 1 min of a given situation's duration? If changes in reaction strength were slower than those in stimulus situation, this would prove that Blackbirds are unable to adapt their behaviour to a given situation at the same rate, and that the general excitation of the bird is too strong for it to control in such a short time. No differences should then be expected between parts 1 and 2 (min 1—5 and 6—10, respectively) of experiments I through VI.
2. Would the Blackbird's reaction strength to mobbing calls playback alone differ from their response to this playback combined with owl presentation? A similarity in the two reactions would suggest that mobbing calls alone have the same activating function as those calls combined with the presentation of the owl.

An analysis was also made of the frequency of alighting and settling on each of the two perches. If the Blackbirds' reactions to stimulus situations were to be merely the result of arousal caused by the movement of the box and presentation of its inside irrespective of its content and localization of the box, the frequency of settling on the perch closer to the box should be similar to that on the more distant one.

The experiments I—VI were conducted on 11 urban and 8 forest birds and only experiment VII was carried out on 10 urban and 7 forest birds. The experiments were conducted in October, November and December. The birds were then 2.5 to 3.5 years old.

The following data were noted during the experiment:

— The number of "duck" calls. This is a call of insecurity characteristic for the species. These "duck" calls (Curio et al. 1978) has been presented on a sonogram in the book by Bergmann and Helb (1982). Some of the birds used in the presented experiments emitted, very seldom, the "tix" call but, these being only very occasional, were not analysed. The "duck" calls were most frequently emitted at alighting on perch.

— The number of alighting on perches, the one closer and the one more distant from the dummy. All flights between the cage floor and the perch terminating with settling on the perch were taken into account here. "1" recorded for alighting on perch or returning to the floor, so, e.g. if a bird alighted on the perch and then flew back down on the floor, "2" was recorded.

— The number of flights between perches. One flight was considered as done if the distance perch — perch had been covered.

— The number of hops, i.e. flights towards a perch which did not result in alighting on the perch. It was quite frequent that a bird flew up to the height of the perch, alighted for a moment on the cage wall and immediately jumped off from it landing on the floor. One hop was counted for each flight betwen: floor and wall, wall and floor, floor and perch (yet without alighting there), perch and wall, wall and perch.

— The number of walks — one "walk" was couted if 2/3 length of the cage were covered in a single direction. Usually a bird turned back after walking from the left side of the cage to the right and covered the same distance in the other direction — this was treated as two walks.

— The number of 10-sec. intervals during which a bird settled on a perch at least once. Here, such intervals were counted irrespectively of the duration of the bird's stay on the perch, be it 1 or 10 secs.

Because of high individual variation in reaction strength and expression of the particular behaviour types, reaction strength was standardized according to Curio et al. (1978), where experiments were conducted with an almost identical procedure on the same avian species.

In calculating reaction strengths, the number of walks, "duck" calls, hops and flights was taken into account. It has been assumed that frequency of each reaction type depends on its threshold value (Andrew 1961 a). A more frequent reaction type has a lower threshold value. It has been established that birds walk on the cage floor when they are little, or not at all, insecure. "Hops" appear on insecurity intensification and are accompanied by alarm calls. Flights occur only during strong alarm. The following standardization indices were assumed for the above activities: walks = 1, "duck" calls — 2, hops = 4, flights = 5 (alighting on perch and flight between them).

Reaction strength was separately calculated for each part of experiments (min 1—5) and after response (min 6—10), and, in the case of experiment VII — part 2, separately for each minute. For each bird, the number of occurrences of a particular action was multiplied by the stated standardization index and thus-obtained values corresponding to the mean standardized reaction strength per min of experiment. A similar value was calculated for the whole groups of urban and forest birds.

2. Results and discussion

In order to check the extent to which the movement of the box alone influences reaction strength and whether it is similar in min 1 (beginning of the experiment) and min 6 (beginning of after response), reaction strengths were calculated separately for those minutes (Table VII). It appeared that reaction strength was always distinctly higher in min 1 than min 6. These differences are significant in all experiments in urban and forest birds with the exception of experiment I. Reaction strength in urban and forest birds alike was also clearly greater in parts 1 (min 1—5) of expts I—VI than in parts 2 (min 6—10) of those experiments (Table VIII). The differences are statistically significant with the exception of expt. III for urban birds.

Table VII

Predator presentation test. Comparison of response strength in 1 st and 6 th mins of experiment

		Experiments					
		I	II	III	IV	V	VI
Urban birds	min. 1	74.18	113.63	161.36	198.09	228.27	215.73
	min. 6	44.90	70.00	75.00	84.18	95.00	79.63
	significance level	NS	0.05	0.01	0.001	0.001	0.001
Forest birds	min. 1	108.12	147.87	130.13	185.38	178.50	153.13
	min. 6	87.25	77.57	62.50	75.12	72.50	71.13
	significance level	NS	0.05	0.01	0.01	0.02	0.01

Table VIII

Predator presentation test. Comparison of response strength in 1st (mins 1—5) and 2nd (mins 6—10) parts of experiments

		Experiments					
		I	II	III	IV	V	VI
Urban birds	(min. 1—5)	31.71	71.11	95.18	136.45	199.89	173.27
	(min. 6—10)	14.98	26.25	45.56	44.13	35.26	21.27
	significance level	0.05	0.05	NS	0.01	0.001	0.001
Forest birds	(min. 1—5)	64.40	82.92	82.48	149.15	141.78	167.93
	(min. 6—10)	43.15	26.60	27.20	15.20	25.30	21.08
	significance level	0.05	0.02	0.02	0.01	0.01	0.01

The results obtained show that the box's rotating movement itself is not the only factor influencing reaction strength. They also give grounds for analysing the Blackbirds' behaviour changes in the particular experiments in terms of reaction to various stimulus situations the birds are able to distinguish.

In urban Blackbirds, initial reaction strength to the empty box was relatively low and increased until expt. III (Table IX). Differences in reaction strength between expts I and II and I and III are statistically significant, while those between expts II and III are not.

In forest Blackbirds, initial reaction strength was higher than in the urban ones and still increasing in expt. II, remaining on the same level until expt. III. However, differences between expts I and III are not statistically significant (Table X).

This growth of reaction strength results from a decrease in reaction strength inhibition to the presented stimulus, as observed already in experiments with handling.

Reaction strengths in urban and forest Blackbirds to the presentation of the owl in the rotating box was clearly higher than that to the box alone (expts IV and I—III, respectively) (Tables IX, X). In urban birds, only the dif-

Table IX

Predator presentation test. Comparison of response strength in part 1 (mins 1—5) of each experiment (I—VII) in urban Blackbirds; statistic significance level included

Experiment	Mean response strength						
I	31.71						
II	71.11	0.01					
III	95.18	0.001	NS				
IV	136.45	0.005	NS	NS			
V	199.89	0.005	0.02	0.05	0.02		
VI	173.27	0.005	0.05	0.005	NS	NS	
VII	150.80	0.005	0.01	0.05	NS	0.02	NS
		I	II	III	IV	V	VI

Table X

Predator presentation test. Comparison of response strength in part 1 (mins 1—5) of each experiment (I—VII) in forest Blackbirds; statistic significance level included

Experiment	Mean response strength						
I	64.40						
II	82.92	NS					
III	82.48	NS	NS				
IV	149.15	NS	0.05	0.05			
V	141.78	NS	NS	NS	NS		
VI	167.93	0.05	0.05	NS	NS	NS	
VII	200.00	0.05	0.05	0.01	NS	NS	NS
		I	II	III	IV	V	VI

ference between expts I and IV is statistically significant, as is also the case with expts I—III and IV in forest ones. In expt V (owl presentation with mobbing calls), reaction strength reaches its highest value in urban Blackbirds: 199.89. This reaction was significantly stronger than in all other experiments with the exception of VI (Table IX), contrary to that in forest Blackbirds, where it remained on a level similar to that in expt. IV. In expt. VI and VII, a fall in reaction strength occurs in urban Blackbirds (VI — 173.27, VII — 150.80) while an increase is observed in forest birds (VI — 167.93, VII — 200.00) (Table X). With the exception of the differences between expts V and VII in urban birds, however, no statistic significance occurs in those variations.

The comparison of standardized reaction strength between urban and forest Blackbirds yielded the existence of statistically-significant differences in reaction strengths only between the initial experiments with empty box presentation ($p = 0.05$).

A comparison was also made of the Blackbird's reaction strength during 1-min repetitions of all experimental situations in part 2 of experiment VII with reaction strength to the identical situations in respective minutes of expts V, VI and VII (Table XI). It was established that reaction strength in particular minutes of that part of the experiment did not differ from that to the same experimental situations in earlier experiments (the differences are of no statistical significance).

Table XI

Predator presentation test. Comparison of the Blackbirds' response strength in 1-min repetitions of experimental situations in experiment VII with similar situations in earlier experiments (V — owl+mobbing calls, VII — owl only, VI — after owl withdrawn). All differences of no statistic significance

Experiment / min.	V / 2nd ↔	VII / 6th	VII / 2nd ↔	VII / 7th	VI / 7th ↔	VII / 9th
urban birds	212.40	221.50	156.30	106.10	13.30	13.10
forest birds	112.43	195.30	165.57	145.70	26.57	0.30

Another comparison concerned reaction strength in the particular minutes of part 2 of expt VII. In urban Blackbirds, all differences observed are statistically significant except for the reaction to the owl presentation without mobbing calls (mean 106.3) and that to mobbing calls playback alone (mean 107.3) (Table XII). In forest Blackbirds, the only significant differences occurred between minutes without owl presentation (min. 8, 9, 10) and with owl presentation with mobbing calls (Table XIII).

Reaction strength in urban Blackbirds was considerably higher than in forest ones to playback of mobbing calls itself, the difference being of statistical significance (Table XIV). This proves that differences in character of the two groups' reactions to mobbing calls playback, which is further suppor-

Table XII

Predator presentation test. Comparison of urban Blackbirds' response strength in particular minutes of part 2 in experiment VII (mins 6—10); statistic significance level included

Min	Mean response strength				
6	221.5				
7	106.1	0.001			
8	64.0	0.001	0.02		
9	19.1	0.001	0.01	0.001	
10	107.3	0.005	NS	0.05	0.01
		6	7	8	9

Table XIII

Predator presentation test. Comparison of forest Blackbirds' response strength in particular minutes of part 2 in experiment VII (mins 6—10); statistic significance level included

Min	Mean response strength				
6	195.3				
7	145.7	NS			
8	68.1	0.05	NS		
9	0.3	0.05	0.05	0.05	
10	47.4	0.05	NS	NS	NS
		6	7	8	9

ted by the following facts. Four urban Blackbirds and only one forest bird responded with mobbing to mobbing calls playback in min 10. In urban Blackbirds, reaction strength to mobbing calls playback with owl presentation was also (in expt. V) significantly higher than the reaction to owl presentation alone. In contrast, response strength of forest Blackbirds to the same stimulus situation did not differ statistically from other experiments with owl presentation (Table VIII).

In forest Blackbirds, statistically significant differences occurred only between experiments with empty box presentation and those with owl presentation. No such differences appeared in reaction strength to the variation of stimulus situation connected with owl presentation. The most characteristic is the fall in reaction strength to owl presentation combined with mobbing calls playback. The behaviour varied in particular individuals. Such a fall occurred in five out of eight forest birds while an increase was observed in the

Table XIV

Predator presentation test. Comparison of mean response strength of urban and forest Blackbirds in part 2 of experiment VII (mins 6—10); mean number of "duck" calls emitted by birds shown for min 10

	Min					
	6	7	8	9	10	
						calls
Urban birds	221.5	106.1	64.0	13.1	107.3	3.6
Forest birds	195.3	145.7	68.1	0.3	47.4	0.8
Significance level	NS	NS	NS	NS	0.05	NS

remaining three. In urban ones, reaction strength decreased from expt. IV to V in two individuals only. The other nine reacted with increased strength. This might be caused by a greater strategy differentiation in forest Blackbirds' reaction. The decrease in forest birds' response is connected with the fact that those birds devote more time to the observation of their surroundings which also occurred in min 10 of expt. VII — during playback of mobbing calls alone. Urban birds reacted to the contrary — by exhibiting a high vocal and movement activity. This was a typical response to owl exhibited by cage birds (Curio et al. 1978).

A comparison of the responses in urban and forest Blackbirds shows that mobbing calls are recognizable by the birds of both populations but constitute for them signals for different behaviour. Forest Blackbirds react to those calls with an increase of vigilance and careful observation of the environment, while urban birds join the mobbing individual. The lack of differences in reaction to expt. II, III (empty box) and expt. IV (owl presentation) suggests that urban birds have no innate ability of owl recognition. On the other hand, the occurrence of statistically significant difference in response to all experiments connected with empty box presentation (I—III) and experiments-tests for learning the recognition of the owl (VI, VII) shows that the Blackbirds have learned to mob the owl, i.e. to recognize it as a predator, and that they have the innate ability to distinguish the function of mobbing calls.

The quicker "calming down" of the urban birds is suggested by the fact of considerable fall in reaction strength in expt. VII between min 7 (owl presentation) and min 8 (withdrawing the owl) in urban birds, which did not appear in forest ones (Table XIII).

The Blackbirds clearly avoided alighting on the perch closer to the place of Tawny Owl dummy presentation. This perch was many times less occupied by both groups of birds, as evidenced by mean setting time on the perch, than the perch more distant from the owl. All differences in part 1 (min 1—5) of each experiment are statistically significant (Table XV, XVI). During after response reaction (min 6—10) the only insiginifant differences were those in

Table XV

Predator presentation test. Mean lengths of stay on perches close and more distant from the owl dummy for urban Blackbirds in all experiments (given as number of 10-sec. intervals)

		Experiments						
		I	II	III	IV	V	VI	VII
Min 1—5	Closer perch	0.05	0.27	0.53	0.81	1.42	0.67	0.62
	More distant perch	2.71	2.80	1.98	2.78	5.04	3.58	3.40
	Significance level	0.005	0.001	0.005	0.001	0.01	0.01	0.01
Min 6—10	Closer perch	0.04	0.78	1.55	1.49	0.73	0.49	
	More distant perch	2.48	2.00	1.95	3.15	3.54	1.89	
	Significance level	0.02	0.05	NS	NS	0.02	0.05	

Table XVI

Predator presentation test. Mean lengths of stay on perches close and more distant from the owl dummy for forest Blackbirds in all experiments (given as number of 10-sec. intervals)

		Experiments						
		I	II	III	IV	V	VI	VII
Min 1—5	Closer perch	0.18	0.10	0.10	0.08	0.38	0.10	0.58
	More distant perch	3.80	1.15	2.63	3.15	4.73	4.30	4.34
	Significance level	0.05	0.05	0.01	0.05	0.01	0.02	0.02
Min 6—10	Closer perch	0.18	0.10	0.68	0.08	0.42	0.05	
	More distant perch	1.78	0.90	2.50	2.40	3.90	2.58	
	Significance level	NS	NS	0.05	0.05	0.02	0.02	

experiments II and IV in forest birds an I and II in urban ones. This proves that the responses of the birds do not result from any undirectional arousal caused by circumstances of experimental procedure and that the birds also react to the spatial context of the experimental situation. This same was evidenced in the field by Shalter (1978a).

Three urban birds and a forest one did not use the closer perch at all. Mean time of stay on this perch in all experiments was calculated for the remaining birds, yielding 0.96 and 0.29 for urban and forest birds respectively. The differences observed are of statistical significance ($p = 0.05$).

Urban Blackbirds adapted much more rapidly to experimental conditions, as evidenced by the much quicker increase in frequency of alighting on the perch closer to the dummy in urban birds from I to VI expts than in the forest ones.

VIII. DISCUSSION

The basic problem in this kind of research consists in stating whether the differences observed in the behaviour of birds are innate, or on the contrary, whether they result from the imprinting by the enviromnent in which the birds remained or became conditioned during ontogenetic development. The following facts show the innate character of those differences. Birds were taken as nestlings from the field, at an age when they could not yet have been negatively conditioned to external objects such as man or predator. Studies on behavioural ontogeny in Blackbirds (Messmer, Messmer 1956) have stated that the critical period when this type of conditioning occurs take place during the acquisition of independent feeding by the birds, i.e. from 14th to 20th day of life. Blackbird nestlings reared by man at that age are later unafraid of man, they treat him as a sexual partner even preferring him to other individuals of their species (Messmer, Messmer 1956). The Blackbirds used in the experiment were at that time hand-fed very rarely in order to make them feed on their own, which ability appeared after 2—3 days. It is also at that time that the Blackbirds radically changed their behaviour on man's appearance in rearing rooms. They interrupted their activities and alertly observed their surroundings. A few days later their behaviour was practically identical with that of wild birds kept in other rooms.

On the other hand, the nestlings could not have undergone imprinting upon the environment in which they remained before being taken for research, as the period in which such conditioning occurs begins much later, i.e. when the nestlings become independent (Bateson 1987, Bischof, Lassek 1985, Schlee 1981).

The innate character of the behaviour observed is indicated by the fact that particular individuals tended to react in the same way to the same stimulus situation, as has been yielded by all experiments. The birds were reared in visual isolation, so they could not connect voices heard with concrete situational context. They could not learn the particular behaviour modes from other individuals. This innateness of behaviour is also indirectly proven by the works show the possibility of selecting animals according to appearance of a given behaviour (Kovach 1979). In the case of majority of behaviour types recorded in the present work, papers by other investigators have demonstrated that the tendency to those behaviours (and their particular intensities) is hereditary (Levine, Broadhurst 1963, McGrath et al. 1972, Gallup 1974, Partridge 1974, 1979, Berthold, Querner 1982).

When considering the problem of birds' adaptation to life in town, one has to take into account the role of ecological factors such as better trophic and breeding conditions on the one hand, and the impact of ethological ones on the other. Of key importance among the latter is the presence of man in towns. Little attention has been paid so far to this problem, and the effect of man's presence was sometimes even neglected as of little relevance, which could lead to obtaining contrary results by various authors and make the continuation of ecological and ethological studies much more difficult if not outright impossible (Buirton 1983, McLean et al. 1985, Grabiński pers. comm.). Man is a predator to birds, one to which their reaction is the strongest, as evidenced by a number of works (Snow 1958, Curio 1959, Knight, Temple 1986). It has been determined in various studies on anti-predator reactions that birds do not mob the predator they fear the most but try to hide and the emit alarm-calls (KERLINGER, LEHRER 1982, LEGER, NELSON 1983, KLUMP, SHALTER 1984). A resting predator discovered by birds is violently mobbed by them. Birds mob a hunting predator if they are able to attack it, often in a big flock (MOHR 1960).

My own observations of mobbing reaction of Blackbirds in the field while recording calls of mobbing the owl (needed for experiments V and VII of predator presentation test) show that urban Blackbirds, in spite of their close visual contact with man, are very vigilant and closely observe man. Forest Blackbirds maintain a much greater escape distance from man and also observe him alertly. The presentation of a stuffed owl caused a similar effect in town and in the forest. In my presence, in town, even if I was standing at 20—30 m from the dummy, the Blackbirds never mobbed it. It is only observer's hiding at a greater distance that caused the mobbing of the dummy after the Blackbird's approach. Blackbirds only emitted alarm calls in my presence. Similar observation have been made by SNOW (1958). In his study of function of mobbing calls caused by man, BUIRTON (1983) established that such a reaction occurs only in relation to a man known to the birds. A stranger is reacted to with alarm calls and sheltering. A similar reaction has also been observed in Blackbirds (SNOW 1958).

These data show that Blackbirds settling in town had to vanquish the strongest ethological barrier connected with a radical shortening of escape distance. The profits from settling in town, i.e. the possibilities of using a plentiful feeding basis, of prolonging the breeding period, of abandoning the costly migration and the much greater survival of adult individuals account for the preference to settle in this environment. On the other hand, however, the reduction of escape distance drastically diminishes, in case of danger perception, the time for decision to escape or stay. This problem could be solved devoting more time to surroundings surveillance (OWENS, GOSS-CUSTARD 1976, LEGER, NELSON 1982). Yet the frequency of surroundings observation resulting from a considerable reduction of escape distance would probably level all profits of settling in town. This is why birds living in town had to undergo a strong selection favouring those rapidly reacting to changes in the environment.

Such changes take place much quicker in an urban environment than in the forest. They are difficult to predict. They are connected with topography, human presence and visual and acoustic pressures. This is why another ability, apart from that of rapid change detection, had to evolve — the ability to rapid change evaluation, closely connected with the learning process. This shows why the ability of learning should be much better developed in urban birds. Facts supporting the above are included in the work by ANDREW (1961a). He has stated that urban birds are better adapted to laboratory conditions than the forest ones.

The results of the present work confirm the above-mentioned assumption. During the open-field test, urban Blackbirds decreased the time devoted to surroundings observation much sooner than the forest ones. A similar phenomenon occurred during tonic immobility and handling tests, when urban Blackbirds sooner exhibited behaviour indicating a lowering of reaction strength connected with adaptation to experimental situation in repetitions of the experimental procedure. Also in the reaction to predator presentation test, urban Blackbirds decreased their reaction strength to withdrawal of the owl dummy (after response) significantly quicker than did the forest ones. The faster adaptation ability of urban Blackbirds is also indicated by the greater frequency of alighting close to the presented predator dummy.

Tonic immobility tests have shown that urban Blackbirds react much more intensive to direct danger situation. Forest Blackbirds reacted less strongly and did not exhibit any response strength change after repetition of experiment — which did happen in urban birds. The faster urban Blackbirds' adaptation is also evidenced by the fact that they emitted distress calls much more seldom than the forest birds did in experiments with handling; these calls indicate the perception of strongest danger. Forest Blackbirds exhibited the state of strong arousal (measured as frequency of beak opening) much more seldom than the urban ones during that test — its conditions must then been evaluated as more dangerous by the forest birds.

The problem of the different reaction of urban and forest birds to owl dummy presentation and mobbing calls playback still requires some consideration. The results obtained indicate an innate ability to distinguish dangerous objects, such as the owl, in forest Blackbirds. In contrast, however, this ability does not seem to be present in urban birds.

The results confirm that Blackbirds distinguish, in an innate way, the function of mobbing calls. Data suggesting the innate ability of recognizing mobbing calls have been obtained for the Pied Flycatcher by CURIO (1975) and for the Blackbird by MESSMER, MESSMER (1956). Yet the quite different reaction of the urban and forest birds to mobbing calls playback shows the different strategies assumed by those birds. Forest Blackbirds reacted with vigilance intensification, some of them remained motionless, while urban birds exhibited mobbing reactions. Likewise, in experiment with handling, forest birds showed a greater alertness than the urban ones. Those different behaviours seem to be adaptive in both environments. Urban Blackbirds, living in dense concentrations face better odds in discouraging an eventual predator by group-mobbing or warning others (FRANKENBERG 1981). The forest ones, on the other hand, living in very small concentration in woods have no possibility of rapid flock formation for a more effective predator mobbing. Also, the risk taken by a single mobbing bird is very considerable and the natural selection does not prefer this sort of behaviour (HAMILTON 1971). An exception to this rule only concerns birds in breeding periods, when mobbing is very intensive in defence of effort invested in breeding (CURIO 1975, SHIELDS 1984, SHEDD 1982). In order to avoid the above situation, research on reaction to predator was conducted outside the breeding period (Oct.—Dec.).

Two alternative hypotheses explaining the mechanism of emergence of urban Blackbird population have been forwarded so far in ornithological literature. One of them assumed the appearance of the urban population on a limited area in Western Europe and its subsequent expansion to other regions (Graczyk 1963). In consequence, the urban population would be genetically isolated from the forest one and the characters observed would be innate. The other maintained that forest Blackbirds have penetrated into towns in many European localities — so the observed adaptations are those of adult individuals and no genetic isolation occurs between the two populations (Tomiałojć 1976).

The present view is that the differences between forest and urban populations are at least partially genetically-based (Tomiałojć 1985). No specific features are named, however, which would differentiate the two groups of Blackbirds. Nor has it been possible to discern morphological variations between the two populations (Graczyk 1961, Havlin 1962). The generally mentioned feature of lesser shyness and shortening the escape distance (Graczyk 1963) has never been studied. Tomiałojć (1976) judged that adult individuals learn that no danger awaits them from man, shorten their escape distance and settle in towns. The silent assumption underlying this view, however, was that all individuals penetrating urban areas have the ability of such adaptation. Nor was the exact meaning of limited shyness concretely defined apart from shortening escape distance.

The author of the present study is of the opinion that limited shyness does not consist in eliminating the fear of man; it should rather be understood as a result of the evaluation of threat from man evaluation and constant adaptation to observed human behaviour.

Although the feature of increased agressiveness in urban Blackbirds is also mentioned (Luniak, Mulsow 1988), it has not been studied — similarly to the problem of limited shyness.

Man is treated by birds as the most dangerous predator; he can penetrate and change all places where birds feed, breed and rest. This is why of all individuals appearing in urbanized areas, only those could settle there, profit from the rich food supply and start breeding, which had the greater innate ability to adapt their behaviour to the constant changes of situation, i.e. the more plastic ones. Such individuals probably occur in all forest populations. Yet populations of forested areas are maintained, by means of natural control factors, at a much lower level than that in urban populations. This is why it should be expected that the penetration of urban environment by forest birds takes more time than the colonization of new town by urban birds.

Urban Blackbirds living in high density must leave, in a large percentage, the urban environment for winter as the availability of food considerably decreases at that time there (Schwabl 1983). Also an intensive dispersion of immature and females individuals occurs after the breeding season. Those birds can penetrate very distant regions. It has been established that the penetration of urbanized environments in autumn-winter season anticipate the appearance of breeding populations (Luniak, Mulsow, Walasz, in print). It should be then expected that the expansion of birds with "urban" characters and able to populate new urban areas will be taking place at a much faster rate than the selection of individuals with "urban" features from forest populations. This seems to be confirmed by the experimental introduction of urban Blackbirds from Poznań (Poland) to Kiev (USSR), where no Blackbirds had been there at all (Graczyk 1974). Since that time, the population of introduced birds has constantly developed in the city (Kostyushin 1983).

When confronted with this, the fact of emergence of new independent urbanization centres might be noticeable only in areas distant from the existing range of urbanized populations. It seems that this phenomenon is presently under way in Alma-Ata and other towns of Kazakhstan (Kowschar, Shujko 1984), where another Blackbird subspecies, *T. m. intermedius* (Richmond 1896), is now undergoing urbanization.

The urban population has emerged as the result of selection of individuals with certain behavioural features, and not as a consequence of the appearance of individuals with totally new characters. The author does not consider it relevant to study the problem whether there exists a strict genetic isolation between the two populations. Ethological factors of selection cause the concentration, in towns, of individuals equipped with such abilities as rapid adaptation to changing conditions, i.e. of birds of greater innate capabilities to learning.

It should not be expected that any greater morphological changes would occur in urban birds, at least in Europe, for the migrations in the area cause a constant mingling of specimens from various regions. Also, the process of suburban zone modification and unarrested growth of urban areas at the expense of the natural environment of the Blackbird is so fast that a constant increase in its urban population and in the zone of mingling of the two populations might be expected, what might eventually inhibit the process of appearance of occasional morphological variations. In addition, an expansion of the urban populations might be expected in suburban and forest areas. This might be further influenced by the decrease in potential predator populations which could threaten urban Blackbirds in forest regions. Finally, the intensified human penetration of forests in the vicinity of towns might cause a greater selective pressure on the elimination of forest individuals with lesser adaptative abilities on the one hand and diminish the pressure of predators on the species on the other.

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STRESZCZENIE

Celem pracy było sprecyzowanie czynników powodujących powstanie w mieście populacji kosów *Turdus merula* o odmiennych przystosowaniach etologicznych oraz zbadanie różnic w zachowaniach kosów miejskich i leśnych — czy różnice te są wrodzone, czy też są jedynie wynikiem adaptacji w czasie rozwoju ontogenetycznego lub u ptaków dorosłych.

Przyjęto, że podstawowymi czynnikami presji etologicznej w środowisku miejskim jest stała obecność człowieka, duże zróżnicowanie bodźców akustycznych i wizualnych oraz częste i nieprzewidywalne zmiany, zachodzące w tym środowisku.

Ptaki do badań zabrano z gniazd kosów miejskich i leśnych. Pisklęta były w wieku 6—10 dni, to jest w wieku, w którym nie mogły jeszcze poznać otaczającego środowiska i zostać na nie uwarunkowane. Wykonano pięć standardowych testów etologicznych. Były to: badania niepokoju migracyjnego, test otwartego pola, test katalepsji, test reakcji na handling i test reakcji na drapieżnika.

Uzyskano wyniki wskazujące na brak wrodzonych różnic w tendencji do migracji ptaków obu populacji w pierwszym roku życia (tab. I, II). Dane te

są zbieżne z wynikami badań terenowych innych autorów i wskazują, że dobór nie działa w kierunku eliminacji zdolności do migracji ptaków miejskich. Umożliwia to odrodzenie się populacji miejskiej po ostrych zimach, które mogą znacznie zredukować populację zimującą.

W teście otwartego pola średni czas trwania poszczególnych czynności obliczony dla sumy eksperymentów I—III był podobny u kosów obu populacji (tab. III). Statystycznie istotne różnice wystąpiły w przebiegu reakcji u samic obu grup. Samice leśne na powtórzenie eksperymentu (II eksp.) zareagowały istotnym zmniejszeniem czasu poświęconego na aktywną obserwację otoczenia i dopiero w eksperymencie III wystąpił wzrost czasu poświęconego na obserwację otoczenia (tab. IV). Samice kosów miejskich natomiast szybciej poznały przestrzeń urządzenia testowego i w trzecim eksperymencie wystąpił spadek czasu poświęcanego na aktywną obserwację otoczenia.

W pierwszym eksperymencie katalepsji kosy miejskie zareagowały znacznie silniej, co objawiło się dłuższym czasem katalepsji. Świadczy to o ich większej reaktywności. W drugim eksperymencie istotnie zmniejszyły czas katalepsji. Czas katalepsji kosów leśnych natomiast był w pierwszym eksperymencie znacznie krótszy niż kosów miejskich i nie uległ zmianie w czasie powtórzenia eksperymentu (tab. V).

W teście reakcji na handling kosy leśne oceniały sytuację eksperymentalną jako bardziej niebezpieczną niż ptaki miejskie, mimo że wszystkie ptaki były wcześniej jednakowo przyzwyczajone do procedury eksperymentalnej. Dowodzi tego mniejsza frekwencja otwarcia dzioba i większa frekwencja krzyków u kosów leśnych w czasie handlingu (tab. VI).

W teście reakcji na drapieżnika siła reakcji ptaków obu grup była istotnie wyższa w części eksperymentalnej niż w czasie reakcji uspokajania (after response) (tab. VIII). Także obrót pudełka, w którym eksponowano wypchanego puszczyka, nie był jedynym czynnikiem wywołującym reakcję ptaków (tab. VII). Zarówno kosy miejskie jak i leśne unikały siadania na drążku bliższym miejsca eksponowania atrapy (tab. XV, XVI). Dowodzi to, że reakcja ptaków nie była wynikiem bezkierunkowego ogólnego pobudzenia w czasie eksperymentu, lecz ptaki reagowały na eksponowany bodziec. Porównanie siły reakcji w czasie jednominutowych powtórzeń wszystkich sytuacji eksperymentalnych w drugiej części eksperymentu VII wykazało, że kosy obu grup zmieniały swoje zachowania w zależności od prezentowanego bodźca (tab. XI, XII, XIII). U kosów miejskich wystąpiło zróżnicowanie siły reakcji, związane ze zróżnicowaniem sytuacji bodźcowej, w czasie eksp. IV—VII (tab. IX), czego nie stwierdzono u kosów leśnych (tab. X).

Wyniki doświadczeń dowodzą silniejszej reaktywności kosów miejskich i jednocześnie zdolności do szybszego uczenia się — dopasowywania zachowań do szybko zmieniających się sytuacji, co jest bardzo ważne w środowisku miejskim.

Uzyskane wyniki potwierdzają hipotezę o wrodzonym charakterze różnic zachowań występujących między osobnikami obu populacji. Wykazują także, że kosy leśne, w odróżnieniu od kosów miejskich, w sposób wrodzony rozpoznają drapieżnika, jakim jest sowa (puszczyk). Kosy miejskie natomiast, tak jak i leśne, rozpoznają w sposób wrodzony funkcję głosów nękania.

Kosy miejskie wykazały w czasie eksperymentów zdecydowanie odmienną strategię reakcji na obecność drapieżnika niż kosy leśne. Ptaki miejskie reagowały wzmożeniem aktywności głosowej i ruchowej (tab. IX, X, XIV), co w naturze mogło przyciągnąć inne osobniki i umożliwić skuteczne odpędzenie drapieżnika. Kosy leśne natomiast na taką samą sytuację eksperymentalną reagowały zwiększeniem czujności i wykazywały zachowania wskazujące na chęć ukrycia się. Tak odmienne reakcje mają znaczenie adaptatywne w obu środowiskach. Kosy miejskie żyją w dużym zagęszczeniu i są w stanie w krótkim czasie ostrzec swoich sąsiadów lub zebrać się w stado, które odpędzi drapieżnika. Kosy leśne natomiast żyją w znacznie mniejszym zagęszczeniu i nie są w stanie zebrać się w stado, które mogłoby skutecznie nękać drapieżnika.

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