

## Variation in Population Parameters: Adaptation to Toxic Environmental Factors

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**Abstract**—Some mechanisms of adaptation of natural populations to toxic environmental factors are discussed. The dandelion and hole-nesting birds are used as examples for demonstrating that an increase in the variation of reproductive parameters upon chemical environmental pollution favors the survival of those individuals in the populations that are better adapted to changes in the climate and other environmental conditions. The increased variation in reproductive parameters may promote the elimination of less fit individuals from populations. The ensuing energy loss is the cost of maintaining the population size in the chemically degraded environment.

**Key words:** ecotoxicology, adaptation, heavy metals, animal and plant populations, variability, reproduction.

The functioning of natural systems under conditions of toxic environmental pollution is the key problem in ecological toxicology. Observations on natural populations seldom reveal the signs of damage that are readily detected in the same species under laboratory or vivarium conditions (*Rasteniya...*, 1983; Bezel', 1987; Pokarzhevskii *et al.*, 2000). Obviously, individual adaptation mechanisms mediated by correction of biochemical and physiological processes, as well as population mechanisms, are responsible for the maintenance of homeostasis in natural systems.

The inherent heterogeneity and functional diversity of individuals in populations are the basis of population adaptation in both animals and plants. Population adaptation to chemical environmental pollution is defined as the ability of natural animal populations and plant cenopopulations to function normally and maintain their size. Adaptation is achieved through selection of individuals that are either the most tolerant toward a given toxic factor or the most fertile, as well as owing to migration from neighboring areas.

In this work, we summarize the data on the plant and animal populations in which general mechanisms of adaptation to chemical pollution of their environment have been studied. The degree of adaptation to toxic environmental factors was estimated from reproductive parameters in plant and animal populations.

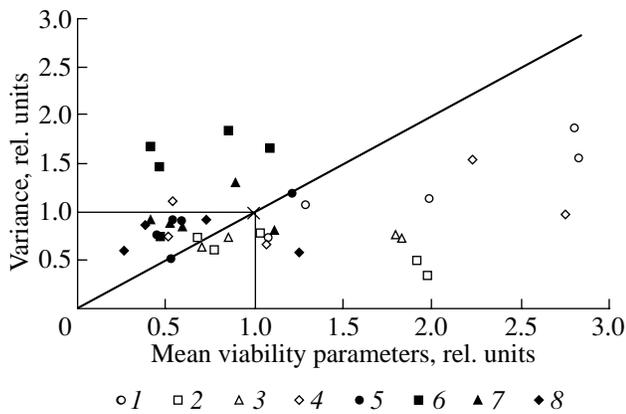
### MATERIAL AND METHODS

The material was obtained during ecotoxicological studies on natural ecosystems contaminated with heavy metals in the Middle Ural region. The objects of the studies were the populations of dandelion (*Taraxacum officinale* s.l.) that had grown for a long time in areas with different degrees of heavy-metal pollution of the

soil and plant cover. This species is polymorphic. In all test plots, two morphological forms prevailed, *T. off. f. dahlstedtii* Lindb. fil. and *T. off. f. pectinatiforme* Lindb. fil. (*Opredelitel'...*, 1994), which clearly differ in the dissection pattern of leaf blade at the generative phase (Bezel' *et al.*, 1998b). The soils were medium-podzolic, with neutral or weakly alkaline pH (6.6–8.7). Geobotanical conditions in the plots were the same, except for the level of pollution with heavy metals (zinc, copper, lead, and cadmium). The contents of chemical elements in soil samples (horizon A1) were determined, after extracting movable forms, by means of atomic absorption spectrometry.

The viability of seed progeny was estimated under laboratory conditions. The seeds were collected from ten plants of each form in every cenopopulation studied. The seeds germinated in distilled water for 30 days, and the following parameters were estimated: seed vigor (SV), germination rate (GR), survival of one-month seedlings (S), root length (RL), and the index of leaf formation (L—the percentage of seedlings with a true leaf among all seedlings survived). These data were processed statistically, including estimation of mean values and variances.

Other objects were the pied flycatcher (*Ficedula hypoleuca*) and the great tit (*Parus major*). The reproductive parameters of hole-nesting birds were studied in three zones with different levels of pollution with the same metals (the impact, buffer, and background zones). We recorded the following parameters in the birds that occupied artificial nests in each zone: (1) the quality (volume) of eggs in a nest; (2) clutch size (the number of eggs per nest); (3) brood size (the number of fledglings per incubated clutch); and (4) the weight of chicks before leaving the nest, which characterizes



**Fig. 1.** The dependence of the variances of viability parameters on their mean values in *T. officinale* s.l. seed progeny. Designations: (1–4) *T. off. f. dahlstedtii*: (1) SV, (2) S, (3) GR, (4) RL; and (5–8) *T. off. f. pectinatiforme*: (5) SV, (6) S, (7) GR, and (8) RL.

their energy resources and prospects for survival after starting to live independently.

The gradient of the total chemical pollution in the test plots was measured as the total toxic load expressed in relative units. This parameter varied from 1 to 33 units for dandelion and from 1 to 4.6 units for the birds. The plots with artificial nests, the habitats of dandelion cenopopulations, and general characteristics of the material obtained have been described in detail elsewhere (Bezel' *et al.*, 1998a, 1998b).

## RESULTS AND DISCUSSION

### 1. Variability of Population Parameters

The variability of reproductive parameters in natural populations may be regarded as the most important criterion of the capacity of living organisms for adaptation to the changing environment. The coefficient of variation (*CV*—the ratio of the mean square deviation to the mean value of the trait) is often used as a measure of the variation of the trait. However, the deviations of individual variants ( $a_i$ ) from the mean value ( $a$ ) may correlate with one another, and *CV* in such a case does not adequately reflect their possible variability. In the context of the problem discussed, the absolute deviation of a trait (variance,  $\sigma$ ) is crucial. From this standpoint, let us consider the relationship between the values of reproductive parameters and their variance. To compare the parameters varying in both value and dimension, we normalized them with respect to the corresponding values obtained at the background plot: the values of each parameter in the background plot were taken as unity, and the values in other plots were expressed as fractions of this value.

If these parameters expressed in relative units are strictly proportional to one another, then there is a linear relationship ( $a = \sigma$ ). This means that the increase or

decrease in the average parameters ( $a$ ) is accompanied by a proportional change in their variance ( $\sigma$ ). If some points are located below the plot of this linear dependence, this means that an increase or decrease in the mean values of population parameters under the effect of changes in environmental conditions is accompanied by a disproportionately smaller decrease in their variation. Conversely, the area above the line  $a = \sigma$  corresponds to the population processes in which changes in the parameters are accompanied by a disproportional increase in their variation.

Data on the viability of dandelion seed progeny illustrate this difference between the responses of natural populations to toxic environmental pollution. Figure 1 shows the relationship between the variance of the parameters of seed reproduction and their mean values in relative units in both forms of *T. officinale* s.l. As is seen from Fig. 1, *T. off. f. pectinatiforme* seeds from the most polluted plots exhibited lower SV, GR, S, RL, and L upon germination in distilled water. However, the variances of these parameters remained above the line  $a = \sigma$  throughout almost the entire range of toxic exposure; i.e., when the reproductive parameters of this form decreased under the effect of soil pollution, their variation increased disproportionately (Zhuikova *et al.*, 1999). A different relationship was observed in *T. off. f. dahlstedtii*, in which seed quality was higher in the most polluted plots. Note that, in contrast to this relationship in *T. off. f. pectinatiforme*, the variance of these parameters decreased disproportionately as the toxic load on the parent plants increased. This resulted in a narrower range of variation in the parameters studied (see Fig. 1).

The problem of adaptation to toxic environmental factors is related to the fact that the dose–effect relationship is a population phenomenon. The heterogeneity of natural populations, which are complex systems of physiologically and functionally different subpopulations, inevitably manifests itself in different responses of these groups to toxic factors (Bezel' *et al.*, 1998a). As we noted above, three ranges of the effective toxic factor may be distinguished in the ecotoxicological dose–effect relationship. At low doses, differences in sensitivity between the intrapopulation groups are insignificant. In this case, the structure and viability of a population remain unchanged, and variation in population parameters remains at the background level, reflecting adaptation to normal environmental conditions.

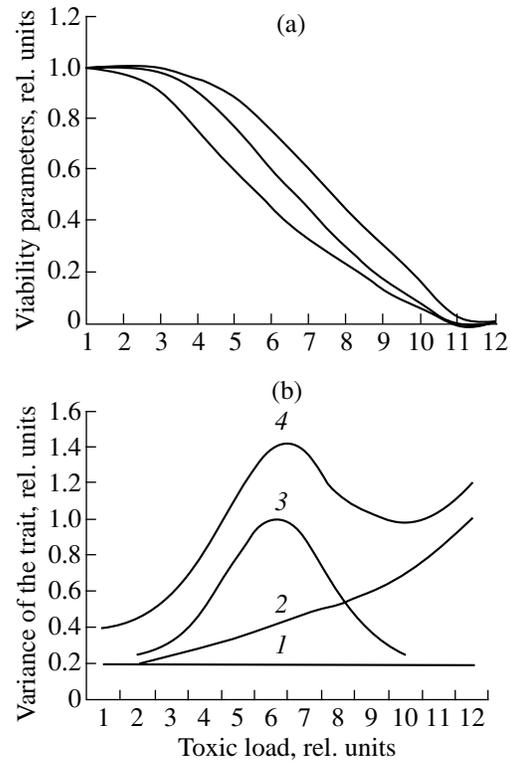
A heavy toxic load results in serious damage to all groups of organisms and elimination of affected individuals, whereas the parameters of viability exhibit a minimum variation. The population heterogeneity with respect to individual tolerance is expressed to the maximum degree in the medium dose range (Fig. 2a), which is therefore of special interest. At these doses, intrapopulation differences provide for elimination of only some individuals from the groups most sensitive to toxic exposure. This selection leads to adaptive changes

in the structure of natural populations. The change in the sex and age composition may affect population dynamics. Thus, an increase in toxic exposure is expected to lead to an increase in the variance of the parameters due to the difference in the sensitivity to toxic factors between intrapopulation groups.

In the background plots, the mean population characteristics, including reproductive parameters, and the range of their natural variation have been established in the course of long-term evolution. This ensures the stable existence of the population and its adequate response to the fluctuations of environmental conditions. Variation in population parameters usually follows a normal distribution. Chemical environmental pollution is a constant additional factor. At the same time, "traditional" environmental factors are also present in polluted areas and they also permanently affect the composition of populations adapted to chemical stress. As a first approximation, we may assume that the resultant variation of population parameters in polluted areas consists of the variance determined by the effect of the toxic factor on the population system that is heterogeneous with respect to tolerance  $[(\sigma_T(P))]$  and the variance determined by fluctuations of environmental conditions  $\sigma_{env}$ :  $\sigma_{\Sigma} = \sigma_T(P) + \sigma_{env}$ .

As we noted above,  $\sigma_T(P)$  does not depend on the toxic load ( $P$ ) monotonically (Fig. 2b). We may assume that the variance of environmental conditions ( $\sigma_{env}$ ) in the absence of toxic load is constant. Under real conditions, natural systems, especially phytocenoses, degrade if toxic loads are high enough (Vorobeichik and Khantemirova, 1994). In this case, the habitats of various species often shift toward the pessimum (the species composition and abundance of the components of phytocenoses decrease, food resources become depleted, and the plots in general become insular). The variation of population parameters caused by chemical degradation of the environment increases along the gradient of the toxic factor; therefore, the environmental variance also must depend on the toxic load:  $\sigma_{env} = \sigma_{env}(P)$ . Figure 2b schematically shows these components and the total variance of the toxic effect as a function of the toxic load.

An adaptive response to this combined exposure implies the retention of individuals adapted to the normal (unpolluted) environment and an increase in the proportion of individuals highly tolerant to a specific toxic factor in the population structure. These requirements inevitably lead to an increased variation in the important parameters determining the vital activity of the population. Both a decrease and increase in the mean population parameters may cause this increase in variation. Thus, the necessity to survive under any conditions "impels" the population to retain the individuals adapted to the normal environment when the population is exposed to additional extreme factors (toxic exposure) that affect its mean parameters. This distorts the normal statistical distribution of the parameters.

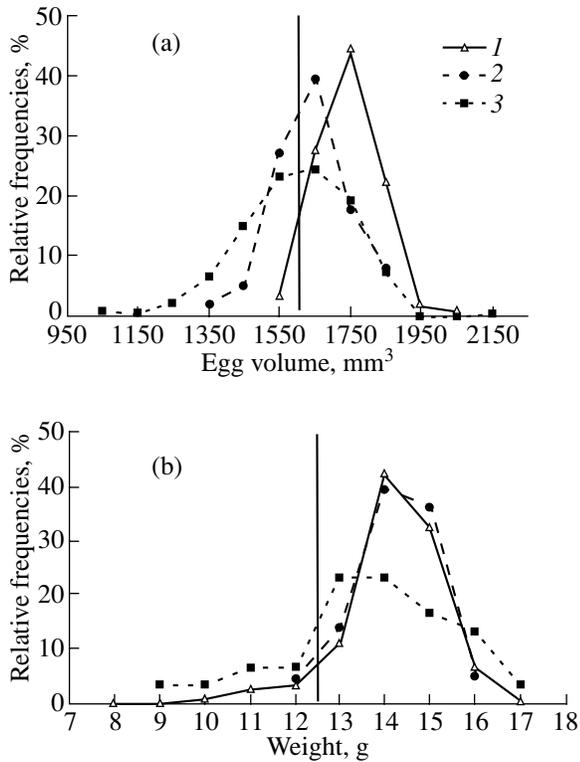


**Fig. 2.** The dependence of (a) viability parameters and (b) their variances on the toxic load: (1) variance under background conditions, (2) variance resulting from chemical degradation of the environment, (3) variance resulting from the direct toxic influence (see Fig. 2a), and (4) the resultant (total) variance of the trait.

We may assume that the larger the overlap of variation curves for the parameters characterizing the "background" and "polluted" parts of the population, the more adequate the response to changes in "traditional" environmental conditions in the population adapted to toxic exposure. It should be taken into account that the individuals most important for the viability of a population adapted to toxic stress are those whose parameters are closest to the modal class of the variation range of background parameters.

The degree of this type of adaptation to permanently varying environmental factors may be formally expressed as  $K = \sum (c_{bgr} \cdot c_{mp})$ . The summation is done over all class intervals of variation ranges that coincide for the background and polluted (impact) areas;  $c_{bgr}$  and  $c_{mp}$  are relative frequencies of these coinciding class intervals, respectively. For maximally adapted populations (a complete coincidence of variation curves), the introduced parameter  $K$  is  $K = \sum c_{bgr}^2$ .

Let us consider the change of the variation curves of egg volumes in great tits and the weight of fledglings in flycatchers living in the background, moderately polluted (buffer), and heavily polluted (impact) areas (Bezel' *et al.*, 1998a) (Fig. 3). Under the toxic load, the



**Fig. 3.** The distributions of (a) egg volume in the great tit and (b) the weight of fledglings in the flycatcher in the (1) background, (2) buffer, and (3) impact zones.

variation curves had a left-hand asymmetry and partially overlapped with background distributions. This allowed us to estimate to what degree these changes in the parameters of eggs and young birds exposed to the toxic factor correspond to the conditions in the background area.

We calculated the parameter  $K$  for the plots studied and found that, in the flycatchers nesting in the impact area, the cohort of fledglings was approximately 37% less adapted to variation in natural environmental conditions compared to the fledglings from the background area. In the buffer zone, the degree of adaptation was the same as in the background zone. The analysis of egg volumes in the great tit demonstrated that their correspondence to natural environmental conditions was decreased by 23 and 45% in the buffer and impact areas, respectively (Fig. 4). Thus, the decrease in egg volume and the weight of fledglings in hole-nesting birds under toxic stress was accompanied by a decrease in their adaptation with respect to these traits.

However, such an adaptation process is sometimes accompanied by the significant improvement of some population characteristics, including reproductive parameters. We found that two morphological forms of dandelion that constituted a single cenopopulation differently responded to toxic exposure with respect to seed quality (Zhuikova *et al.*, 1998, 1999). Seed vigor,

germination rate, survival of seedlings, and the parameters of leaf formation and root length were different in *T. off. f. pectinatiforme* and *T. off. f. dahlstedtii* from the plots with different degrees of pollution. Upon an increasing toxic load, seed viability in the former consistently decreased and variation in the parameters studied increased. The situation was different with *T. off. f. dahlstedtii*, in which the seeds of the plants growing in the polluted plots were more viable (see Fig. 1), with the variances of these parameters decreasing disproportionately (Zhuikova *et al.*, 1998). The fact that *T. off. f. dahlstedtii* did not entirely displace the other form indicates that the latter may prove to be more resistant to both increased concentrations of metals and other environmental factors.

Naturally, the introduced adaptation index  $K$  for the entire set of parameters in these two forms must change differently along the gradient of toxic load (Fig. 5). The mean parameters of seed reproduction and the corresponding values of  $K$  on the background segment of the curve were assumed to be unity. In *T. off. f. pectinatiforme*, the degree of adaptation to possible variation in environmental conditions consistently decreased as the mean values decreased. In the other form (*T. off. f. dahlstedtii*), virtually all viability indices increased; however, the adaptation of the seed progeny to changes in "traditional" factors consistently decreased.

## 2. Elimination of the Less Fit from the Population

The change in the variation of the main population parameters due to toxic exposure may have other consequences. Most common is elimination from the population of the marginal individuals that are not adapted to environmental conditions and, hence, do not contribute to the maintenance of population size. In this case, we may postulate that there is a certain range of values beyond which defective individuals are partly eliminated from the population. This elimination of extreme variants has been noted by many researchers for various objects, including the eggs of the great tit, Arctic tern (Myand, 1988), and rook (Bolotnikov *et al.*, 1985). It is known that chicks often do not hatch out of small eggs or, if they do hatch, their development is retarded. We (Bezel' *et al.*, 1998a) demonstrated that the proportion of small, defective eggs in great tits from the impact zone was  $36.2 \pm 4.8\%$  vs.  $11.5 \pm 1.5\%$  in the background area (Fig. 3a).

The chicks whose weight at the moment of leaving the nest is too small to allow them to live independently are eliminated from the population (Bel'skii *et al.*, 1995a, 1995b). The analysis of young flycatchers before they left the nest demonstrated that their distribution with respect to body weight had a left-hand asymmetry in all the plots studied (Fig. 3b). The proportion of chicks with a low body weight (12.5 g is the critical value) in polluted zones was significantly higher than in the control ( $15.3 \pm 4.8$  and  $5.5 \pm 1.3\%$ ,

respectively). Note one phenomenon that partly counterbalances the adverse effect of environmental pollution. If the direct toxic effect characteristic of the heavily polluted zone is accompanied by an insufficient food supply, the death of the less fit chicks helps the rest of the brood to survive. According to our data for the impact zone (Bezel' *et al.*, 1998), the weight of the young flycatchers in small broods (less than four chicks per nest) was significantly higher than in medium and large broods (four or more chicks):  $14.72 \pm 0.19$  g vs.  $13.63 \pm 0.33$  g.

We do not exclude that the large number of less fit fledglings in polluted areas resulted not only from the direct toxic effect on adult birds and chicks but also from an indirect effect on parental pairs. Possibly, less competitive adult birds are mainly displaced to disturbed areas. In this case, the indirect effect of chemical pollution is mediated by the same population mechanisms.

The proportion of normal seeds in the progeny of *T. officinale* s.l. from the polluted plots changed in the same way. Analysis of seedling development until the stage of true leaf in dandelion families demonstrated that the proportion of these families varied from 0 to 72% in different variants. We may conventionally distinguish the families with lower (less than 20%) and higher (more than 20%) parameters of leaf formation. In *T. off. f. dahlstedtii* and *T. off. f. pectinatiforme* growing in the background plot, the ratios between the numbers of families with such parameters were 6 : 4 and 3 : 7, respectively. In the polluted plots, the situation was reversed: *T. off. f. dahlstedtii* exhibited higher parameters due to the elimination of less fit seedlings from the seed progeny, and leaf formation was suppressed in *T. off. f. pectinatiforme* (Pozolotina *et al.*, 2000). The analysis of root length in families yielded similar results.

The data obtained may be regarded as evidence for selection in the dandelion populations. As a result of this selection, *T. off. f. dahlstedtii*, which has better growth characteristics, establishes itself in the polluted areas. Although *T. off. f. pectinatiforme* has a low seed viability, it proved to be resistant to the effect of metals (Zhuikova *et al.*, 1999). This allows the two forms to coexist under the toxic exposure.

In hole-nesting birds, the critical values used in this study were inherently objective (the minimum weight of fledglings and the egg volume), whereas the critical values of L and RL in dandelion were chosen arbitrarily. However, it is conceivable that there are some objective population mechanisms in both cases. On the one hand, they are responsible for changes in the variation of the parameters studied; on the other, they stimulate the elimination of extreme variants. This ensures the survival of the part of the population that is capable

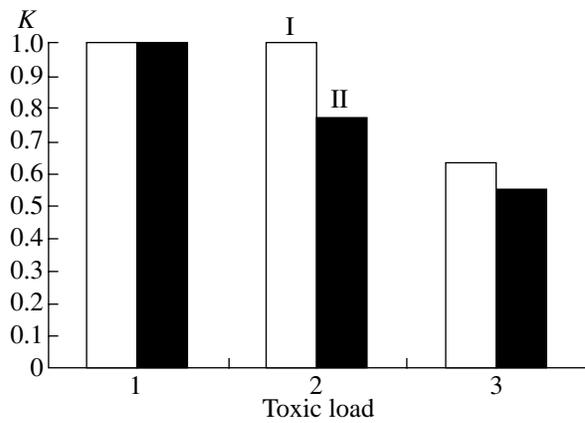


Fig. 4. Changes in adaptation indices (K) for (I) pied flycatcher fledglings and (II) great tit eggs upon chemical pollution of the environment. Zones: (1) background, (2) buffer, and (3) impact.

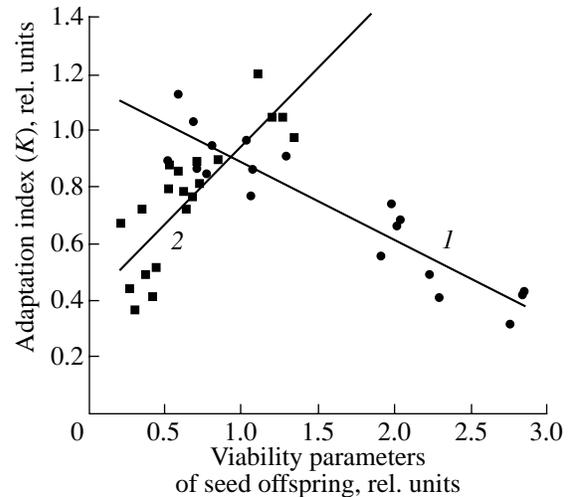
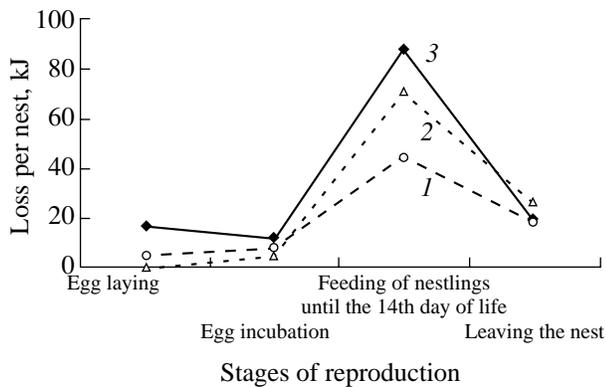


Fig. 5. The dependence of adaptation index (K) on the quality of seed progeny in (1) *T. off. f. dahlstedtii* and (2) *T. off. f. pectinatiforme*.

of maintaining population size in the case of variation in natural and toxic factors.

The process of purification from defective individuals allows us to estimate population losses upon exposure to extreme environmental factors, which is an important characteristic of adaptation. Since the parameters studied are essentially different, it is suitable to express this estimation in energy units. Figure 6 shows the estimations of energy losses in flycatchers during the nesting period. The numbers of eliminated eggs and chicks were recalculated in biomass units, and the mean weights of eggs and 14-day-old birds in the background area were determined. Assuming the energy contents of eggs and chicks in passerine birds to be 1.1 and 1.7 kcal/g fresh weight, respectively (*Populyatsionnaya ekologiya...*, 1982), we calculated the energy



**Fig. 6.** Energy losses during pied flycatcher reproduction in the (1) background, (2) buffer, and (3) impact zones.

loss per nest. The energy of biomass synthesis and parents' energy expenditures for procuring food were not taken into account. Only successful nests were used in the analysis. The losses at the stage of egg laying in polluted zones were calculated relative to the mean clutch size in the background area. This parameter was calculated for each zone at the incubation stage by subtracting the mean number of hatchlings from the mean clutch size in the given zone. The losses at the stage of rearing were calculated as the difference between the numbers of hatchlings and fledglings. The losses during transition to independent life were estimated from the proportion of young birds with body weight below 12.5 g. This weight indicated that the young were emaciated and the probability of their survival was low (Bel'skii *et al.*, 1995; Bezel' *et al.*, 1998a).

According to our data, these energy losses in the local group of flycatchers in the polluted area were 1.5 times higher than in the background area. If we take into account abandoned clutches, the energy loss in the impact zone is even greater. The increased elimination of eggs and chicks is actually the cost that the local group pays for the possibility to bring up a high-quality progeny. We simplify the meaning of "quality," as we only took into account the weight of chicks without regard to the effects of toxicants accumulated in their bodies. This "cost of the offspring quality" does not mean "the cost of the possibility of reproduction" of the local group because the number of fledglings in some species, including the flycatcher, is insufficient for maintaining the population size in disturbed areas. As we noted above, the existence of such species in the zones of strong industrial impact is maintained due to annual migrations.

Thus, the change in variation of major population parameters is one of the mechanisms ensuring efficient adaptation of natural animal and plant populations to chemical pollution of the environment.

The increased variation observed in the populations of hole-nesting birds and dandelion cenopopulations in response to the environmental shift toward the pessimism due to chemical pollution favors the survival of individuals that are better adapted to changing environmental conditions. On the other hand, a decrease in the variation of population parameters indicates that the population has partially lost its capacity for adequately responding to fluctuations of climatic and other natural factors.

The increased variation in reproductive parameters may cause an increased elimination of the less fit. These losses are the cost of the possibility of maintaining population size in the chemically degraded environment.

#### ACKNOWLEDGMENTS

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