

Developmental stability and population dynamics of shrews *Sorex* in central Siberia

Vladimir M. ZAKHAROV, Dmitry V. DEMIN, Alexander S. BARANOV,
Vyacheslav I. BORISOV, Alexey V. VALETSKY and Boris I. SHEFTEL

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We examined temporal variation in developmental stability measured by fluctuating asymmetry of 10 skull characters in sympatric populations of three shrew species: *Sorex araneus* Linnaeus, 1758, *S. caecutiens* Laxmann, 1788 and *S. tundrensis* Merriam, 1900 from one locality in central Siberia with a high four-year-cycle of small mammals. Simultaneous significant changes in developmental stability have been revealed during a population cycle 1986–1989 for all three, most abundant shrew species in the locality. The highest asymmetry for all these species occurred in the year of maximal density. Similar high asymmetry was found for the separate samples of two other species: *S. roboratus* Hollister, 1913 and *S. isodon* Turov, 1924, collected in a peak year 1989 only. The maximal density in 1989 corresponded to the lowest level of breeding success and developmental stability and, *vice versa*, minimal density in 1986 was accompanied by the highest level of breeding success and developmental stability. These data suggest that overpopulation caused by high density of various small mammals adversely affects an organism's condition. Thus, developmental stability may be used to monitor possible changes in a population even in cases where direct estimation of fitness is difficult.

N. K. Koltzov Institute of Developmental Biology Russian Academy of Science, Vavilov Str. 26, Moscow 117808, Russia (VMZ, DVD, ASB, VIB, AVV); Institute of Evolutionary and Ecological Problems Russian Academy of Science, Leninsky prospect, 33, Moscow, 117071 Russia (BIS)

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Introduction

Population dynamics is still one of the basic problems in the population ecology of mammals (Krebs and Myers 1974, Krebs and Wingate 1985, Sadykov and Benenson 1992, Gurnell 1995). The crucial questions are: (1) How does an organism's condition change with population dynamics? (2) Are these changes in an organism's condition correlated with density? (3) How do biotic and abiotic factors influence population dynamics? (4) Does density limit population growth?

Developmental stability study may provide an answer, as it provides an integrate information on various factors adversely affecting an organism's condition in natural populations (Zakharov *et al.* 1991). Developmental stability analysis of two populations of shrews having different types of dynamics has shown that in a cyclic population in central Siberia, developmental stability is negatively correlated with density. In a noncyclic population in southern Finland, there is indication for a positive correlation between these parameters (Zakharov *et al.* 1991). All these data suggest the autoregulation cyclicality for the first population, where high density is the main factor adversely affecting an organism's condition, leading to a population decline. In the second population, higher density corresponds to better condition of animals and environmental factors prove to be the main limitation for the population growth.

The tasks of this study are: (1) to verify the hypothesis whether the tendency for the negative relation between developmental stability and density and positive relation between breeding success and developmental stability are universal for the cyclic populations, and (2) to check if these negative relationships are valid for the cyclic populations of other sympatric species of shrews.

Material and methods

We studied shrews from central Siberia (the eastern bank of the river Yenisei, near the Northern Ecological Station of the Institute of Evolutionary and Ecological Problems, Russian Academy of Sciences; 62°N, 89°E). Regular four year cyclicality has been established for small mammals of this locality (Sheftel 1983, 1989). The study period 1986–1989 corresponds to one cycle starting from the year of minimal density 1986 and finishing by the year of high density 1989. Sympatric populations of eight shrew species occur at this locality. We studied a cycle, 1986–1989, that was unusual in that the regular population increase, which commonly takes place in the third year of a cycle, was interrupted in 1988 by a density decline for all species (Fig. 1).

Annual samples for the whole study period include three most common shrew species: *Sorex araneus* Linnaeus, 1758, *S. caecutiens* Laxmann, 1788 and *S. tundrensis* Merriam, 1900. Only

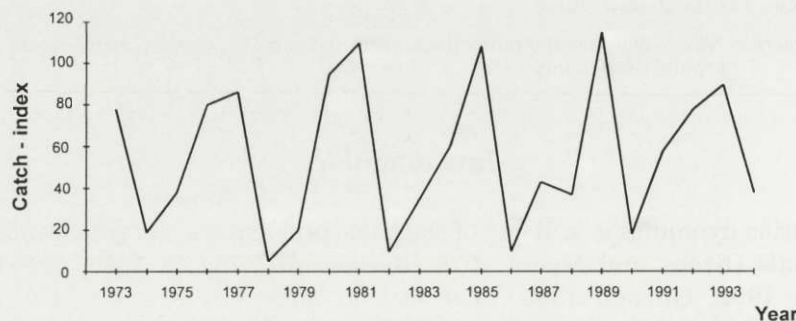


Fig. 1. Population dynamics of 8 shrew species in central Siberia. Catch index – a number of specimens caught by 100 traps per night.

separate samples for the year of high density (1989) for two other species: *S. roboratus* Hollister, 1913 and *S. isodon* Turov, 1924 were available for the analysis. The annual trapping period was July–August. See Sheftel (1989) for the description of the trapping techniques.

Catch index was used as a density estimate that was calculated as a number of specimens caught by 100 traps per night. The ratio between the number of immature shrews and the number of breeding adult specimens caught during the summer was used as a breeding success index.

Developmental stability was estimated by fluctuating asymmetry of ten skull characters (Fig. 2). All characters and their asymmetries were uncorrelated with each other. In this study as well as in the previous one (Zakharov *et al.* 1991) we found no significant directional asymmetry or antisymmetry (definitions in Van Valen 1962, Soulé 1967, Palmer and Strobeck 1986). Mean number of asymmetrical characters per individual was used as an integrated measure of developmental stability (Leary *et al.* 1983, Zakharov 1987, 1989). Young immature shrews were analysed. Samples of males and females for each year were pooled as no sex differences were found in the parameters studied. We used *t*-test for intersample comparison (Sokal and Rohlf 1991).

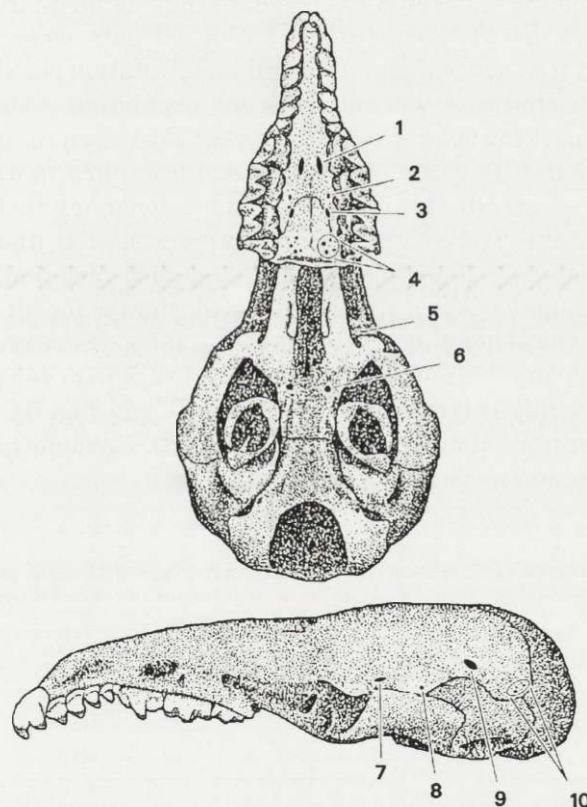


Fig. 2. Cranial characters, as a number of foramina (1–10) examined in the common shrew *Sorex araneus*: 1 – foramen palatinum anterior, 2 – foramen palatinum posterior accessorius minor, 3 – foramen palatinum posterior, 4 – foramen palatinum laminae, 5 – foramen accessorius canalis pterigoideum, 6 – foramen basisphenoidalis lateralis, 7 – foramen parietale anterior, 8 – foramen parietale media, 9 – foramen parietale posterior, 10 – foramen parietale corner.

Results

The integrated developmental stability measure (mean number of asymmetrical characters) showed significant changes ($p < 0.001$, t -test) during a population cycle in the most abundant shrew species in the locality, the common shrew *Sorex araneus*. Asymmetry increased from the year of minimal density to the year of maximal density (Table 1 and Fig. 3). Similar significant increases in asymmetry ($p < 0.01$) with the density increase were seen for two other shrew species: *Sorex caecutiens* and *S. tundrensis* (Table 1 and Fig. 3). As only four years of data were available for analysis, it was not possible to assess the correlation between asymmetry and density, but a tendency for the parallel changes of the parameters was visible for all these species.

For *Sorex araneus* some data have been obtained earlier (Zakharov *et al.* 1991). Developmental stability was estimated in that study by fluctuating asymmetry of 13 skull characters. To get comparable results, all data were recalculated and presented as mean frequency of asymmetrical manifestation per character. Despite some difference in character set and different population cycles studied, mean asymmetry index per character proved to be very close even in absolute values (it changed from 0.22 to 0.44 in 1977–1982 yrs and from 0.26 to 0.41 in 1986–1989 yrs) and showed, generally speaking, the same dynamics in both time series compared. Similar data were obtained for two other species under study: *S. caecutiens* and *S. tundrensis*. In spite of some interspecies variation, asymmetry was the lowest in 1986, and reached its highest level, similar for all species, in 1989, ie at the peak of the population cycle. Even in 1988, when strict cyclicity was interrupted by a density decline, we revealed the change in developmental stability coincided with breeding success alteration (Table 1 and Fig. 3). For *S. roboratus* and *S. isodon*, represented only in samples for 1989, asymmetry values are very close to those for other species in this year.

Table 1. Integrated measure of developmental stability (NA \pm SE) of 10 skull characters (see Fig. 2) in 5 shrew *Sorex* species, collected from the sympatric populations in central Siberia in different years.

Species	Years							
	1986		1987		1988		1989	
	<i>n</i>	NA	<i>n</i>	NA	<i>n</i>	NA	<i>n</i>	NA
<i>S. araneus</i>	20	2.60 \pm 0.26	20	2.90 \pm 0.28	20	3.80 \pm 0.35	20	4.10 \pm 0.25
<i>S. caecutiens</i>	20	2.70 \pm 0.25	20	2.55 \pm 0.24	20	2.90 \pm 0.26	20	4.00 \pm 0.35
<i>S. tundrensis</i>	20	2.05 \pm 0.37	20	3.00 \pm 0.31	20	3.60 \pm 0.25	20	4.00 \pm 0.27
<i>S. roboratus</i>	–	–	–	–	–	–	17	4.00 \pm 0.32
<i>S. isodon</i>	–	–	–	–	–	–	20	3.57 \pm 0.21

Thus, asymmetry, which is an index of developmental stability, revealed the same regular changes during different population cycles in one species and during the same population cycle for different species of shrews.

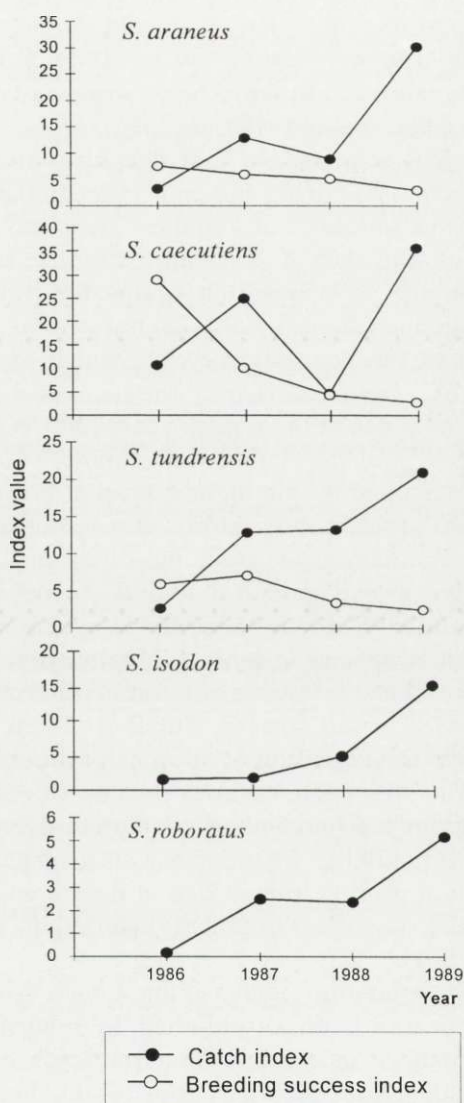


Fig. 3. Population dynamics (catch index – a number of specimens caught by 100 traps per night) and breeding success index in sympatric populations of 5 shrew *Sorex* species in central Siberia in 1986–1989.

Discussion

Population growth can be limited by external environmental conditions or by overpopulation, through autoregulatory mechanisms (Koshkina and Korotkov 1975, Shilov 1977, Christian 1978, Sheftel 1989). Both environment and density

interact in complex ways, but the prevalent effect of each can be distinguished by the simultaneous study of density and organism's condition. In the case of environment dependent regulation, high density would correspond to better environmental conditions and organism status. In the case of density dependent regulation, high density would correspond to the worse organism status and population decrease. Previous study of developmental stability as an index of an organism's condition in *Sorex araneus* has already illustrated both of these cases described (Zakharov *et al.* 1991).

This study show that decreases in developmental stability with increasing density seen during one cycle in a population of a common shrew in central Siberia are not unique, but regular. They can be seen for this population in another population cycle 3 years after the first study period. Similar changes can also be seen during population cycles for different species. The latter support the prediction (Sheftel 1989, Zakharov *et al.* 1991) that social stress during the peak year of the population cycles, which are synchronous for various species at the locality, can be caused by the increased density of different small mammals. The maximal density in a peak year, 1989, corresponded to the lowest level of breeding success and developmental stability. Conversely, minimal density in 1986 was accompanied by the highest level of breeding success and developmental stability for all species under study. In establishing the adverse effect of high density on an organism's condition for different species, we illustrate the importance of studying developmental stability, which can reveal the mechanism of population dynamics. Without these data, synchronous population dynamics for all small mammal species in central Siberia can be interpreted as a result of environmental fluctuations: favorable environmental conditions could correspond to a population increase for all species. But there is an opposite effect – high density adversely affects the condition of animals of different species.

This approach assumes that we can use developmental stability to distinguish different mechanisms of population dynamics. A negative correlation of developmental stability with density corresponds to an adverse effect of overpopulation, while a positive correlation of developmental stability with density indicates the crucial role of environmental conditions in population dynamics (see Zakharov *et al.* 1991).

Experimental evidence for a decrease of developmental stability under social stress has been established in laboratory rats (Valetsky *et al.* 1997). The importance of changes in organism's condition, as detected by a decrease in developmental stability, was established by the simultaneous study of various measures of developmental homeostasis: morphogenetic instability under social stress impact in rats accompanied by changes in immune status (Pronin *et al.* 1997), and overpopulation in vole populations adversely affected cytogenetic homeostasis (Dmitriev *et al.* 1997). In the previous study of shrew population dynamics, positive correlation of developmental stability with breeding success

indicates that breeding success is affected by physiological condition of breeding females (Zakharov *et al.* 1991)

In this study we analyzed an unusual cycle, 1986–1989, where the regular population increase, that commonly takes place in the third year of a cycle, was interrupted in 1988 by a density decline for all species (Fig. 1). This decline was probably caused by weather conditions. In spite of this exceptional situation in 1988, when strict cyclicity was interrupted by a density decline, there was still a positive relation of developmental stability with breeding success for all species. This relation suggests that developmental stability is indeed an important population parameter.

There are some advantages to applying developmental stability measures instead of commonly used fitness estimates, such as breeding success index. For example, developmental stability is more sensitive, as it is possible to reveal adverse changes in organisms before serious changes in demographic patterns appear. Second, it is easily applied, as needed information can be obtained through the analysis of one sample of specimens from the population under study. Even museum collection is sufficient for this purpose, instead of the whole breeding season study needed for the correct estimation of breeding success. Finally, more adequate information on the condition of pregnant females and their progeny is available through developmental stability study, as breeding success estimates could reflect not only changes in an organism condition, but also predators or climate pressure, etc.

Thus, developmental stability could be recommended as an approach useful for a wide application to monitor possible changes in a population's condition for various species and to distinguish among mechanisms of their population dynamics.

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