

THE BIOINDICATIVE AND PROGNOSTIC SIGNIFICANCE OF SEX RATIO IN CARABIDAE (INSECTA, COLEOPTERA)

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Abstract

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The relation between the sex ratio of a species and its rank in a species spectrum subjected to various degrees of anthropogenous pressure is studied. Five types of distribution of the sex ratio within the species spectra are distinguished. Their causes are explained and they are put into the wider frame of the *r*—, *S*—, *K*— continuum concept. The approximative prognostic model based on the sex ratio is proposed and verified. The bioindicative and prognostic applicability of sex ratio in *Carabidae* is confirmed.

One of the most striking effects of the anthropogenous influencing animal and plant communities is, with a some exceptions, the decrease in their alpha-diversity. This phenomenon is explicated, as a rule, by a different degree of ecological tolerance in individual species constituting a community. The less tolerant species are expelled from a community by the anthropogenous factors. Conversely, the more tolerant species are advantaged and they can reach a predominant position in their thropical levels. If we consider the following facts, viz., the influence of external temperature and humidity on sex differentiation (Statelov, 1936), (Yntema, Mrosowski, 1982), the internal factors (Hrubešová et Sláma, 1967; Abdel-Malek et Adha, 1978; Hanker et Taimir, 1973; Zuska, 1973, a lot of examples see Schwerdtfeger, 1968), the different preferenda to various factors (Schwerdtfeger, 1968; Thiele, 1977 and others), the tendency of the females to search for habitats close to the ecological optimum of this species (Schwerdtfeger, 1968; Müller, 1970) and the inspecificity of higher or lower tolerance in one or the other sex (see the above authors), we may presume that both sexes will react differently also on anthropogenous factors. So we can presume that the sex ratio and consequently, the intrinsic rate of population growth will change in individual species of a community subjected to anthropogenous pressure. This presumption offers a question, whether and how the changed sex ratios can participate on structural changes of an anthropogenously influenced community. Beside, the question of bioindicative and prognostic applicability of the sex ratio arises. The

4 Table 1. Review and short characteristics of the geobiocoenoses studied and the equations of the regression curves of the dependence of sex ratio in *Carabidae* from the rank of a species in a taxocoenosis

Locality	Year	Veg tier	Characteristics of the geobiocoenosis (groups geobiocoenosis)	Equations of the regression curves of sexual index (SI) and rank of a species (<i>i</i>)
Natural forest geobiocoenoses of the oak to oak-beech veg. tiers				
Moravian Karst, the valley of Řička river	1979	2-3	<i>Fraxini-Alnetra</i>	$SI = -0.0347 + 0.0147 \ln i$
Moravian Karst, the valley of Řička river	1979	1-2	<i>Carpini-Acereta</i>	$SI = -0.0483 + 0.0242 \ln i$
Moravian Karst, the valley of Řička river	1979	3	<i>Tiliae-Acereta</i>	$SI = -0.0294 + 0.0135 \ln i$
Moravian Karst, the valley of Řička river	1979	3	<i>Querci-Fageta tiliae</i>	$SI = -0.0274 + 0.0131 \ln i$
Moravian Karst, the valley of Řička river	1979	2	<i>Fagi-Querceta</i>	$SI = -0.0041 + 0.0043 \ln i$
Pavlovské kopce hills, Děvín	1971	1	<i>Carpini-Querceta</i>	$SI = -0.0012 - 0.0017 \ln i$
Pavlovské kopce hills, Děvín	1981	1	<i>Carpini-Querceta</i>	$SI = 0.0024 + 0.00001 \ln i$
Pavlovské kopce hills, Děvín	1971	2	<i>Fagi-Querceta</i>	$SI = -0.0566 + 0.0251 \ln i$
Pavlovské kopce hills, Děvín	1981	2	<i>Fagi-Querceta</i>	$SI = 0.0576 - 0.0231 \ln i$
Pavlovské kopce hills, Děvín	1971	3	<i>Tiliae-Acereta superiora</i>	$SI = -0.0191 + 0.0096 \ln i$
Pavlovské kopce hills, Děvín	1981	3	<i>Tiliae-Acereta superiora</i>	$SI = 0.0281 - 0.0119 \ln i$
Pavlovské kopce hills, Děvín	1971	2-3	<i>Tiliae-Acereta inferiora</i>	$SI = 0.0071 - 0.0025 \ln i$
Pavlovské kopce hills, Děvín	1981	2-3	<i>Tiliae-Acereta inferiora</i>	$SI = -0.0021 + 0.0015 \ln i$
Pavlovské kopce hills, Děvín	1971	2	<i>Fagi-Querceta</i>	$SI = 0.0148 - 0.0043 \ln i$
Bolehradice, Přední kouty	1971	1	<i>Corni-Querceta</i>	$SI = 0.0263 - 0.0104 \ln i$
Bolehradice, Přední kouty	1971	1	<i>Corni-Querceta</i>	
Natural forest geobiocoenoses of the beech to norway spruces-beech-fire veg. tier				
Buchlovice, Holý kopec hill	1970	3	<i>Querci-Fageta</i>	$SI = 0.0257 - 0.0121 \ln i$
Žákova hora, Žďarské vrchy (mount.)	1971	5	<i>Abieti-Fageta</i>	$SI = 0.0395 - 0.0193 \ln i$
Františkova myslivna, Jeseníky mountains	1971	6	<i>Abieti-Fageta</i>	$SI = 0.0637 - 0.0306 \ln i$
Šrámková, Malá Fatra mountains	1982	5	<i>Aceri-Fageta</i>	$SI = 0.0406 - 0.0171 \ln i$

Field ecosystems

Dolní Sukolom, Uničovská rovina lowland	1963	2	beet	$SI = 0.0155 - 0.0053 \ln i$
Dolní Sukolom, Uničovská rovina lowland	1964	2	beet	$SI = -0.0515 + 0.0216 \ln i$
Střelnice, Uničovská rovina (lowl.)	1963	2	beet	$SI = -0.0246 + 0.0103 \ln i$
Střelnice, Uničovská rovina (lowl.)	1964	2	beet	$SI = 0.0468 - 0.0204 \ln i$
Paseky, Uničovská rovina (lowl.)	1963	2	beet	$SI = -0.0048 + 0.0025 \ln i$
Paseky, Uničovská rovina (lowl.)	1964	2	beet	$SI = -0.0198 + 0.0093 \ln i$
Žemberovec, Ipeľská pahorkatina collines	1981	1	vineyard	$SI = 0.0170 - 0.0051 \ln i$
Báb, Nitrianska pahorkatina collines	1981	1	tobacco	$SI = 0.0409 - 0.0143 \ln i$
Pezinok, Malé Karpaty	1981	1	maize	$SI = 0.0409 - 0.0143 \ln i$
Urban geobiocoenosis close to the natural geobiocoenoses				
Vydrica, Mlynská dolina valey	1982	1	littoral <i>Alnetum</i>	$SI = 0.2086 - 0.0939 \ln i$
Stiminy, Bratislava, K. Ves	1982	1	anthropogenously influenced oak forest with <i>Robinia pseudoacacia</i>	
Lužánky, Brno	1978	0	lowland forest turned to urban park	$SI = 0.0452 - 0.0175 \ln i$
Lužánky, Brno	1979	0	lowland forest turned to urban park	$SI = 0.0657 - 0.0259 \ln i$
Anthropogenously influenced urban gardens and parks				
Břenkova street, Brno	1976	2	urban garden	$SI = -0.0449 + 0.0105 \ln i$
Břenkova street, Brno	1978	2	urban garden	$SI = -0.1160 + 0.0618 \ln i$
Lišeňská street, Brno	1978	2	orchard on the urban periphery	$SI = 0.0120 - 0.0130 \ln i$
Lišeňská street, Brno	1979	2	orchard on the urban periphery	$SI = -0.0447 + 0.0224 \ln i$
Čertova Rokle, Brno-Lesná	1978	2	erosive furrow turned to a park	$SI = -0.1951 + 0.1292 \ln i$
Hakenova street, Brno-Lesná	1978	2	erosive furrow turned to a park	$SI = -0.0476 + 0.0391 \ln i$
Spilberk, Brno	1978	1-2	park on the place of the former fortifications	$SI = -0.0109 - 0.0067 \ln i$

raison d'être of these questions is supported by the striking predominance of females in the dominant species of field ecosystems studied recently in South Slovakia which evidenced more characters of anthropogeneous influence (Šustek, 1983 a, b, c; Povolný and Šustek, 1983).

The aim of the present paper is an attempt at a solution of the above problems. The family *Carabidae* represents a very suitable model group for this aim due to the extensive material and due to the tendency to a balanced sexility in individual species (Schwerdtfeger, 1968; Petruška, 1966; Novák, 1967; Thiele, 1977 and others).

Material and methods

The *Carabidae* included into this study were sampled in 20 forest and in 9 field ecosystems in Moravia and Slovakia and in 11 urban ecosystems in Bratislava and Brno. About 65 000 individuals of *Carabidae* are included in this study. The review and a short characteristics of individual sampling ecosystems is shown in Tab. 1. The material from Moravian Karst was sampled by Dr. J. Vašítko and it was identified by the author. As for the material from beet fields near Dolní Sukolom, Střelice and Paseky see Petruška (1966).

The beetles were sampled by pitfall traps during a whole vegetation period. The 1 liter glass jars with a diameter of 95 mm filled with 4 % formalin solution were used as traps. The beetles dropped into the traps were taken once a month. The number of traps in one geobiocenosis depended upon its surface. Ten traps were exposed in the majority of natural geobiocenoses and five traps were exposed in the majority of urban geobiocenoses.

The sex ratio is calculated for methodical reasons by two formulae. For the descriptive aims, the following formula is used

$$SI = \frac{f_i - m_i}{N} \quad (i = 1, 2, 3, \dots, j - 1, j),$$

where f_i is number of females of the i -th species and m_i is number of males of the i -th species, N is the individual number of all species in a community (sample) and j is the total number of species in this community. This formula is used due to the increasing binar character of the sex ratios in less abundant species or in the species represented only by one individuum respectively. So, each sex ratio is weighed by the dominance of a species in a community. The values of sex ratio calculated by the above formula may fluctuate theoretically between -1 and $+1$, however, they fluctuate within the limits close to 0, if the equity of a community is high. For the aims of calculating a population growth and competition rate, the sex ratio is calculated by the formula

$$SI = \frac{f_i - m_i}{f_i + m_i}$$

The symbols in the formula are the same as in the first case. The values of sex ratio can fluctuate between -1 and $+1$. The balanced sex ratio is expressed by 0. The values of the sex ratio are plotted into the diagrams accordingly to the sequence of the decreasing individual number of species in a community. The distribution of the sex ratios within species spectra is described by logarithmic regression equations (Tab. 1).

The dependence of sex ratio from the rank of a species in *Carabid* taxocenoses in various types of ecosystems

The sex ratio of *Carabidae* in natural geobiocenoses of oak to beech vegetation tiers is rather unpredictable after the rank of a species in a taxocenosis. The males and females predominate alternatively without any dependence from the rank of a species in a taxocenosis. The regression curves (Tab. 1, Figs. 1—15) characterizing

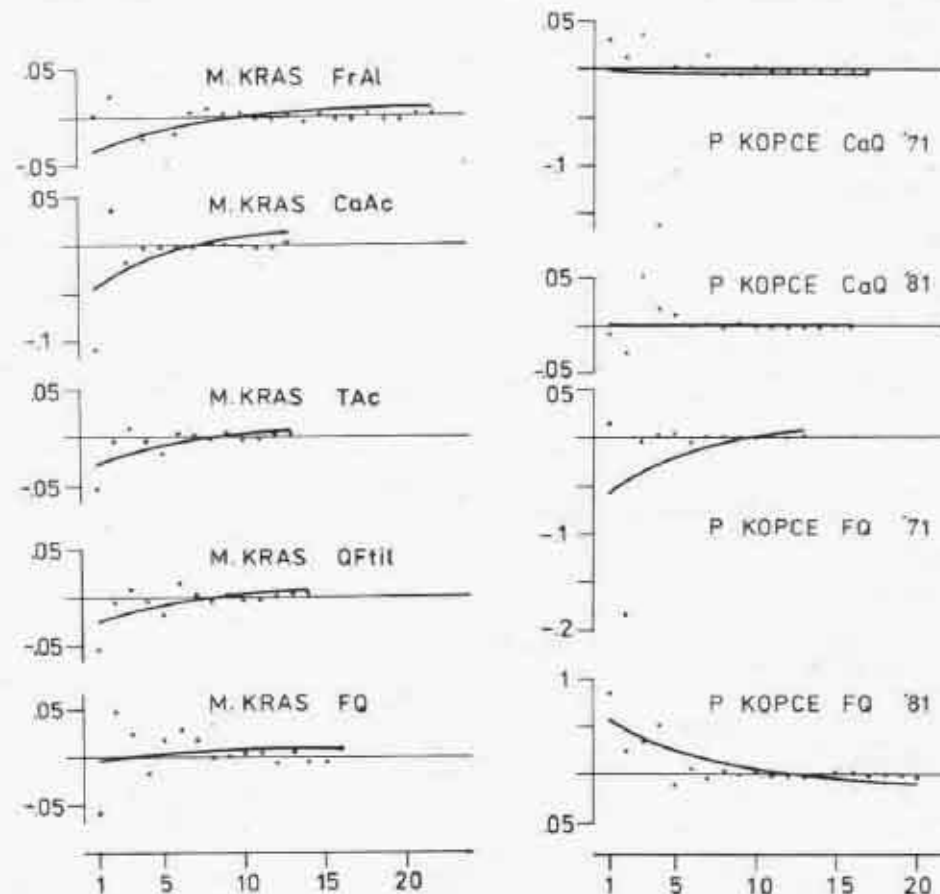


Fig. 1—5. Dependence of sex ratio in *Carabidae* from the rank of a species in a community in the natural forest geobiocenoses in Moravian Karst (1 — FrAl, 2 — CaAc, 3 — TAc, 4 — QF til, 5 — FQ), ordinate — sex ratio, abscissa — rank and number of species in a community.

Fig. 6—9. Dependence of sex ratio in *Carabidae* from the rank of a species in a community in the natural forest geobiocenoses in Pavlovské kopce hills (6 — CaQ 1971, 7 — CaQ 1981, 8 — FQ 1971, 9 — FQ 1981), ordinate and abscissa as in Fig. 1.

the distribution of sex ratios in a taxocenosis are flat and slightly increasing. In the taxocenoses from FQ, TAc, and TAc, studied in the years 1971 and 1981, the form of regression curves changed during both years due to a slight predominance of females in abundant species. In the taxocenoses from FQ and CoQ in Boleradice, the females predominate in abundant species.

In natural ecosystems in beech to norway spruce-fir-beech vegetation tiers the females predominate in first three to four species in all taxocenoses (Tab. 1, Figs. 16—19). The succeeding species have a balanced sex ratio and the males predominate successively in less abundant species. The regression curves decrease steeply.

In a natural lowland forest (Tab. 1, Fig. 24), the sex ratios are unpredictable after

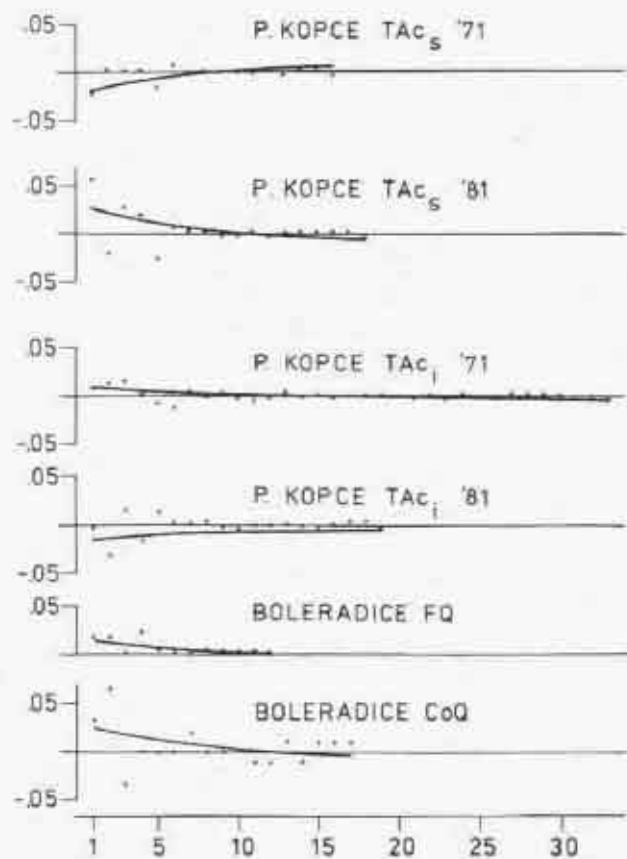


Fig. 10—15. Dependence of sex ratio in *Carabidae* from the rank of a species in a community in the natural forest geobiocenoses in Pavlovské kopce hills and in Boleradice (10 — TAc, 1971, 11 — TAc, 1981, 12 — TAc, 1971, 13 — TAc, 1981, 14 — FQ, 15 — CoQ), ordinate and abscissa as in Fig. 1.

the rank of species in the taxocenosis similarly as in natural forests of oak to oak-beech vegetation tiers. Both sexes in all species tend to a good balance. The regression curve is approximately linear and parallel with the abscissa.

In the geobiocenoids of lowland forests (Tab. 1, Figs. 20—23), the females predominate strikingly in first four species and they tend to a predominance in the whole of a first half of species spectrum. The only exception is represented by *Abax ater* in the alluvium of Vydrica creek (Fig. 20), where the males predominate. It is due to a low width of the alluvium and due to its surrounding by the remnants of

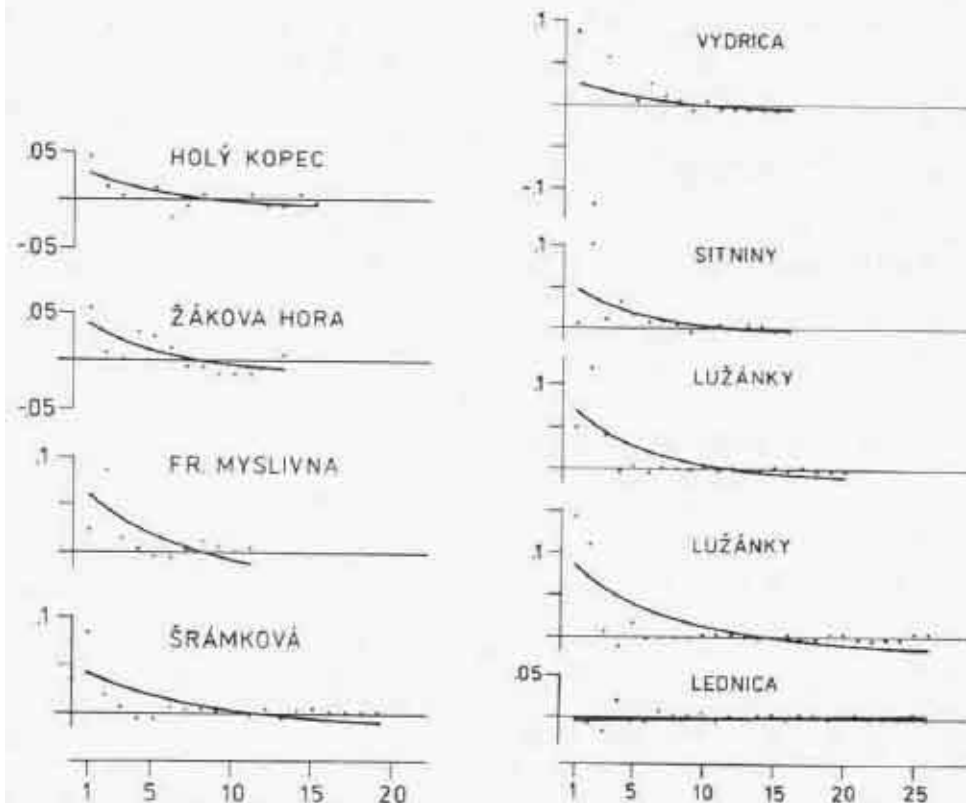


Fig. 16—19. Dependence of sex ratio in *Carabidae* from the rank of a species in a community in natural forest geobiocenoses in beech to norway spruce-beech-fir vegetation tier (16 — Holý kopec hill, QF, 17 — Žákova hora, AF, 18 — Františkova myslivna, AF, 19 — Šrámková, AcF), ordinate and abscissa as in Fig. 1.

Fig. 20—24. Dependence of sex ratio in *Carabidae* from the rank of a species in a community in forest geobiocenoids in Bratislava and Brno and in a natural lowland forests near Lednica (20 — alluvium of Vydrica creek in Bratislava, 21 — Sitniny, Bratislava, 22 — Lužánky 1978, Brno, 23 — Lužánky 1979, Brno, 24 — Lednica, UFr), ordinate and abscissa as in Fig. 1.

oak forests, where *Abax ater* is dominant and where from the more movable males migrate into the alluvium. A similar distribution of sex ratios is seen in the taxocenosis of the oak geobiocenoid in Sitniny. The regression curves decrease, they are very steep and crooked.

In the field ecosystems (Tab. 1, Figs. 25—33) two groups of taxocenoses can be distinguished. The first group is represented by taxocenoses from a tobacco field in

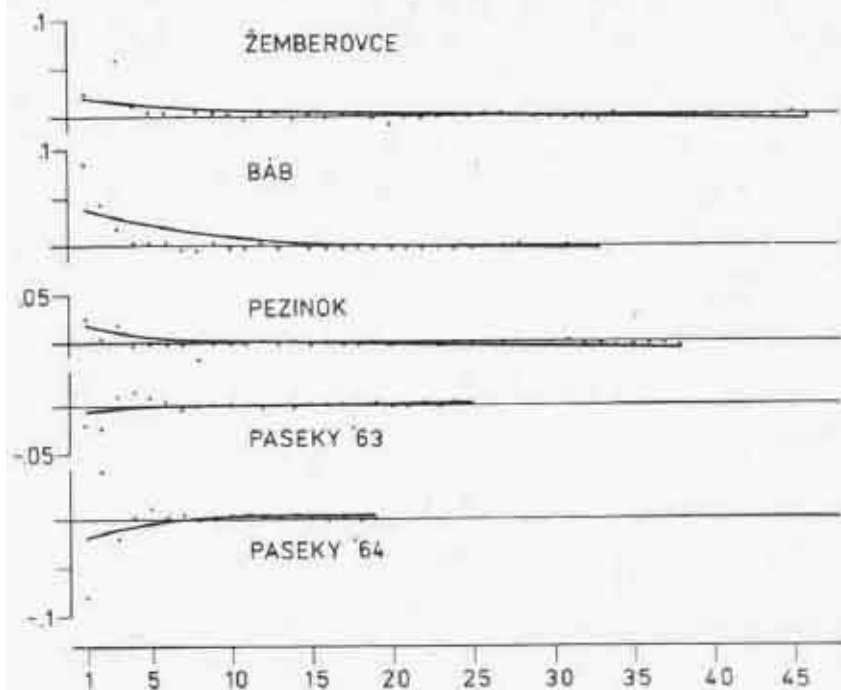


Fig. 25—29. Dependence of sex ratio in *Carabidae* from the rank of a species in a community in field ecosystems (25 — Žemberovce, vineyard, 26 — Báb, tobacco, 27 — Pezinok, maize, 28 — Paseky 1963, beet, 29 — Paseky 1964, beet), ordinate and abscissa as in Fig. 1.

Báb, from a maize field in Pezinok and from a vineyard in Žemberovce (Figs. 25—27, Tab. 1). In all these taxocenoses the females of the first three to four species predominate and the females of following 8—10 species tend to predominate. The sex ratios in the following part of species spectra is balanced and the males predominate at the end of the spectrum. The relatively linear regression curves decrease. The second group of the taxocenoses is represented by the taxocenoses from sugar beet fields at Uničovská rovina lowland studied during 1963—1964 (Petruška, 1966) (Tab. 1, Figs. 28—33). Similarly as in the forests of

oak-beech vegetation tier the sex ratios are unpredictable after the rank of a species in a taxocenosis. The predominance of the females alternate with the predominance of males in the whole of a species spectrum. The regression curves are decreasing and increasing as well. They frequently change their form in two consequent years.

In the urban gardens and parks (Tab. 1, Figs. 34—40) the males predominate

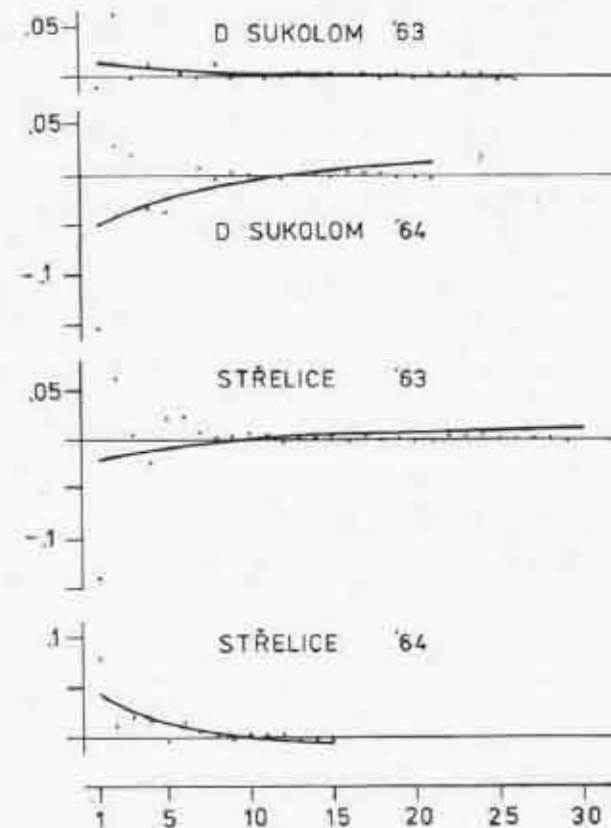


Fig. 30—33. Dependence of sex ratio in *Carabidae* from the rank of a species in a community in field ecosystems (30 — Dolní Sukolom 1963, beet, 31 — Dolní Sukolom 1964, beet, 32 — Střelice 1963, beet, 33 — Střelice 1964, beet) ordinate and abscissa as in Fig. 1.

nearly in all species. Less abundant species tend slightly to little more balanced sex ratios. The regression curves increase strongly in a majority of cases. If they decrease so a greater part of them is situated deeply under the abscissa.

Typization and interpretation of the regression curves of the *Carabid* sex ratio in individual types of ecosystems

Five types of the dependence of the *Carabid* sex ratio from the rank of a species in a taxocenosis can be obtained if the average and the standard error of parameters of the regression equations are calculated for individual types of ecosystems (Figs. 41—45).

Type A with the equation

$$SI = (0.005719 \pm 0.029797) + (0.003369 \pm 0.012989 \ln i)$$

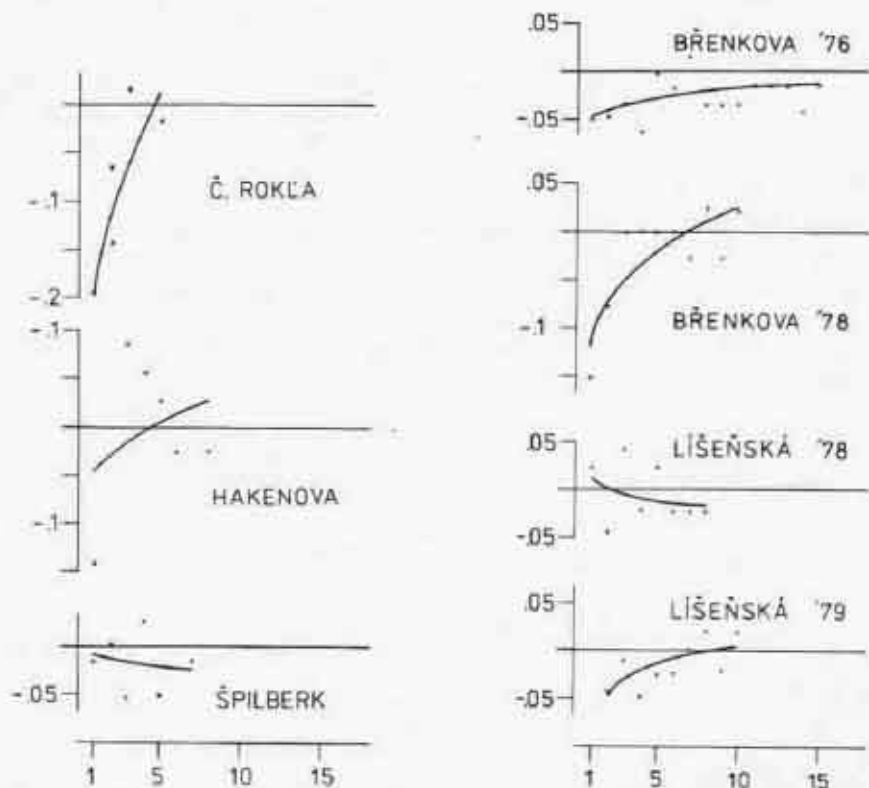


Fig. 34—36. Dependence of sex ratio in *Carabidae* from the rank of a species in a community in urban ecosystems (gardens and parks) (34 — Brno, Čertova Rokfa, 35 — Brno, a hollow near Hakenova street, 36 — Brno, south slope of Schpielberg), ordinate and abscissa as in Fig. 1.

Fig. 37—40. Dependence of sex ratio in *Carabidae* from the rank of a species in a community in urban ecosystems (gardens and parks) (37 — Brno, Břenkova str., 1976, 38 — Brno, Břenkova str., 1978, 39 — Brno, Lišeňská str., 1978, 40 — Brno, Lišeňská str.), ordinate and abscissa as in Fig. 1.

characterizing rather flat curve parallel with the abscissa corresponding to balanced sex ratio of *Carabidae* in natural forest ecosystems of 1.—4. vegetation tiers.

Type B with the equation

$$SI = (0.100475 \pm 0.073671) - (0.041925 \pm 0.035099 \ln i)$$

characterizing the decreasing, steep and crooked curve corresponding to taxocenoses in anthropically influenced ecosystems in 1.—4. vegetation tiers and in lowland forests. The initial point of the curve has the y-coordinate close to 0.1.

Type C with the equation

$$SI = (0.042375 \pm 0.01575) - (0.019775 \pm 0.0078202 \ln i)$$

characterizing the decreasing, relatively sheer and crooked curve corresponding to sex ratio in taxocenoses in natural forest ecosystems in 4.—6. vegetation tier. The initial point of the curve has the y-coordinate close to 0.05. The curve is rather similar as in the type B.

Type D with the equation

$$SI = (0.004333 \pm 0.032163) - (0.004138 \pm 0.011582 \ln i)$$

characterizing relatively flat, slightly decreasing curve, nearly parallel with the

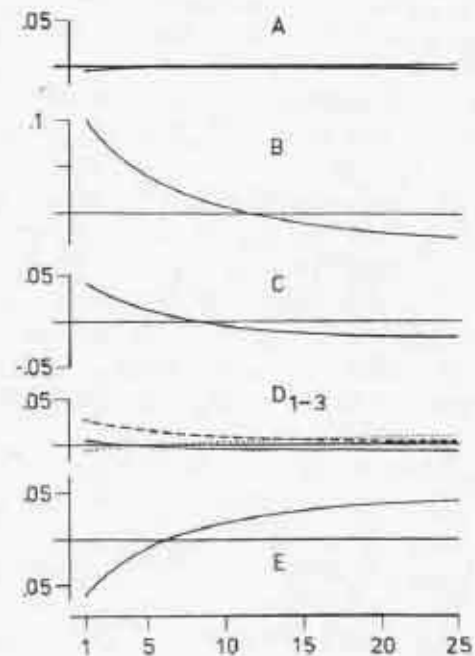


Fig. 41—45. Types of the regression curves of *Carabid* sex ratio in dependence from the rank of a species in a community in various types of ecosystems (41 — A, type of natural forest geobiocenoses in 1.—3. veg. tier, 42 — B, type of the forest geobiocenoids in 1.—3. veg. tier, 43 — C, type of the natural forest geobiocenoses in 4.—6. veg. tier, 44 — D, type of field ecosystems, full line — D₁, basic type, dashed — D₂, subtype of the taxocenoses from first half of sixties, pointed — D₃, subtype of recently studied field ecosystems, 45 — E, type of very influenced urban ecosystem), ordinate and abscissa as in Fig. 1.

abscissa corresponding to the taxocenoses in field ecosystems. In the frame of this type two following subtypes can be distinguished:

Subtype D₂ with the equation

$$SI = (-0.0064 \pm 0.034226) + (0.00298333 \pm 0.014533 \ln i)$$

corresponding to taxocenoses in more preserved field ecosystems or for the taxocenoses studied several years ago respectively.

Subtype D₃ with the equation

$$SI = (0.0258 \pm 0.013162) - (0.008633 \pm 0.004957 \ln i)$$

corresponding to taxocenoses in recently studied field ecosystems. The subtype D₂ inclines to the type A and the subtype D₃ inclines to the type C.

Type E with the equation

$$SI = (-0.063885 \pm 0.070116) + (0.034757 \pm 0.049007 \ln i)$$

characterizing the abruptly increasing curve, situated in its greater part under the abscissa, corresponding to the taxocenoses in the urban gardens and parks exposed to an intensive human activity.

The five types of sex ratio distributions described can be interpreted as follows. The *Carabidae* tend generally to a balanced sex ratio. They can preserve this property only in such conditions where the anthropogenous and abiotic factors do not reach such intensity which could be of selective effect in the different ecological tolerance of both sexes. Hence, in more predictable conditions or if the predominance of females is not necessary for balancing a higher off-spring mortality. The ratio of abundance or biomass of individual species in such communities is determined by a mutual competition of the species in a community or by the competition of the species of the same trophical levels (e.g. *Lycosidae*, Thiele, 1977; some *Silphidae*, Šustek, unpublished). Some indications of a slight predominance of males in such taxocenoses (slightly increasing curves) can be explained by a higher movability of the males. The real sex ratio will be probably more balanced than recognizable by pitfall trapping. Contrary, in less predictable conditions more intensive anthropogenous or abiotic pressures can effect selectively different ecological tolerance of both sexes and the species with more tolerant females start to predominate in such taxocenoses. The interpretation of the predominance in females admits also other explanation, viz., the necessity to balance a higher mortality increasing under unpredictable conditions. This interpretation corresponds to the position of a species in *r*—, *K* — continuum, or in *r*—, *S*—, *K* — continuum respectively. The species reacting on higher anthropogenous or abiotic pressures by a predominance of females are “*r* — selected”. The species with the tendency to predominating males are “*K* — selected” under such conditions. These facts correspond to the increase in the dominance of small sized

Carabidae in field ecosystems from seventies, hence, the species having one of the essential characters presupposed by *r*-selection (Šustek, 1983c).

Another case is represented by taxocenoses in urban gardens and in parks where males predominate. The predominance of males in such taxocenoses can be explained by their insularity. The populations of species constituting such taxocenoses permanently enriched by the immigration of individuals from the surrounding landscape. The males predominate evidently among these immigrating individuals due to their higher movability. The immigration character of the urban *Carabid* taxocenoses is demonstrated also by a higher serological heterogeneity of insects in the urban sed landscape (Tietze, in litt). Hence, in this case, the predominance of males in such taxocenoses can not be considered as an indication of a decrease in population densities, but it indicates the permanent immigration. The ability of expeditious and repeatable occupation of free ecological niches, especially in the initial succession stadiums (the typical case of urban ecosystems), is also one of characters typical of *r*-selection. So, all deviations of the curves of the sex ratio from the types A, D₁ and C indicate an increase in representation of the *r* — selected species. Therefore, the deviations of sex ratio in a *Carabid* taxocenoses from the normal stand characteristic for individual types of natural or for secondary homeostazed communities can be considered, in the same degree, as an indicator of higher influence by anthropogenous or by other unpredictable factors. The sex ratio appears to be more indicative than some other criteria due to its larger biological interpretability.

The possibilities of prognostic application of sex ratio of *Carabidae*

If the sex ratio changes in some species in a community and if these changes seem to be constant, we may presume that also the mutual ratio of such species will change. Such changes depend from mutual competition pressures, from the intrinsic growth rates of individual species, from the currying capacity of ecosystems and from migrations. These factors can be estimated only with difficulties in nature. The carrying capacity cannot be fully used. The intrinsic factors inhibiting the population growth are not known in the majority of economically indifferent species. So, if we wish to attempt at a prognosis of the development of a taxocenosis based on the sex ratios of individual species, we must accept some simplifications:

1. If a community is constant and if the representation of individual species does not change, we can presume that the fertility of females will be constant. We can consider, under above presumption, that the only factor affecting the intrinsic rate of population growth will be the excess or deficiency of females. These presumption corresponds with relatively constant numbers of eggs in individual *Carabid* species (Thiele, 1977). The high predominance of females is obviously not an

inhibitor of population growth due to frequent polygamy in insects (1♂:6–8♀ in *Culicidae*, Abdel-Malek et Ahmed, 1973; 4♂♂:6♀♀ in *Lymantria dispar* during acrescence, Schwerdtfeger, 1968). So we may write

$$r \approx SI_i,$$

there, r is the intrinsic growth rate and SI_i is sex ratio.

2. According to Levins (1968) in Poole (1974) the approximate estimate of the competition can be based on the biomass dominance which, in ecologically near species, indicates the portion of the use of the common ecological niche. Another measure of a mutual competition can be, of course, also the increase (or decrease) in abundance of populations of other species sharing the same thropical level. According to presumption 1., also this increase (or decrease) can be expressed approximately by the sex ratio. So it can be presumed that the competition pressure of more abundant species with more balanced sex ratio will be approximately equal to a pressure of less abundant species with higher predominance of females. Consequently, the competition coefficient α_{ij} (Poole, 1974) can be approximated tentatively as an average sex ratio weighed by biomass of the species, viz.:

$$\alpha_{ij} = \frac{\sum_{i=1, j=1}^{i-1, j} r_i m_i}{\sum_{i=1, j=1} m_i} \quad (1)$$

where m_i is biomass of the i -th species, r_i is the intrinsic rate of the population growth and $i=1, 2, \dots, j-1, j$ is the species number. It can be postulated consequently that the population of the i -th species will increase or decrease dependently from the difference of intrinsic growth rate r_i and of the competition coefficients α_{ij} , viz.:

$$N_{(i)} = N_{0i} \exp r_i - \alpha_{ij}. \quad (2)$$

This approximation is close to some simple models presented by Barymann (1981). It does not include, however, the intrinsic factors inhibiting the population growth of i -th species. If we consider that the i -th species displaced all other species from the same ecological niche and if it itself occupied it, it may be expected that the population growth of this species will be stopped:

$$\alpha_i = r_i. \quad (3)$$

So, the intrinsic growth rate of i -th species can be introduced into the calculation of the competition coefficient α_{ij} and the formula (1) will change as follows:

$$\alpha_{ij} = \frac{\sum_{i=1}^j r_i m_i}{\sum_{i=1}^j m_i} \quad (4)$$

The member (or its more developed forms):

$$\frac{K_i - N_i}{N_i} \quad (5)$$

used in differential forms of logistic formulae will be compensated by the above step.

The mode itself of the calculation of the prognosis by the above formulae will consist calculation of values $N_{(i)}$ after N_{0i} and α_{0ij} . On the basis $N_{(i)}$ the new competition coefficients N_{0ij} will be recalculated and the values $N_{(i)}$ will be established. These steps may be repeated till the values N_{0i} for the required time n are obtained. The individual numbers may be used for the calculations and the biomass as well. The BASIC programm executing all calculations is available by author.

The present model can be used only for species without overlapping generations. This precondition is, however fulfilled in Central European *Carabidae*.

For the verification of the above model the Carabid taxocenosis from the geobiocenosis FQ in Pavlovské kopce hill (Šustek, 1983) was chosen. The reasons for its choice were the striking changes in its structure during 1971–1981, and the presence of all dominant species during both 1971 and 1981. It makes possible a control of observed (real) and theoretical (predicted) representation of individual species. Seven species concentrating 98 % of biomass of all taxocenoses were included into the calculations. Their sexual ratios and biomass are presented in Tab. 2.

Table 2. The values used for the calculation of the prognosis of the representation of seven *Carabid* species based on their sex ratio and biomass in the *Fagi Quercetum* in Pavlovské kopce hills

Species	SI	M 71.	M 81.	M 81.
<i>Abax ater</i>	0.0375	35.76	68.44	74.15
<i>Abax parallelus</i>	-0.0281	12.80	14.50	8.83
<i>Carabus cancellatus</i>	-0.1881	35.22	3.94	4.86
<i>Carabus ullrichi</i>	-0.2000	4.54	0.15	0.55
<i>Carabus coriaceus</i>	0.0715	23.08	26.36	43.10
<i>Carabus nemoralis</i>	0.0196	17.72	26.40	19.71
<i>Carabus hortensis</i>	0.1428	0.89	11.04	3.37
Summ		150.01	150.83	154.57

SI — sex ratio, M — biomass in grams, r — real values, c — theoretical values.

When comparing the values observed during 1971 and 1981 with the values predicted for 1981 by the model, the model obviously overrated the predicted biomass of *Carabus coriaceus* and a little also the biomass of *Abax ater*. This results generally in an underrating of the biomass in other species with increasing

populations. The overrating of *C. coriaceus* is caused probably by neglecting the migration in this model. This explication is supported by approximately the same sex ratio of *C. copriaceus* in two neighbouring geobiocenoses, viz. CaO and TAc, (Šustek, 1983) which caused an adequate increase in individual number and in biomass of *C. coriaceus*. The other factors, e. g. the competition of non-carabid animals were potentially effective, but their evaluation is impossible on the level

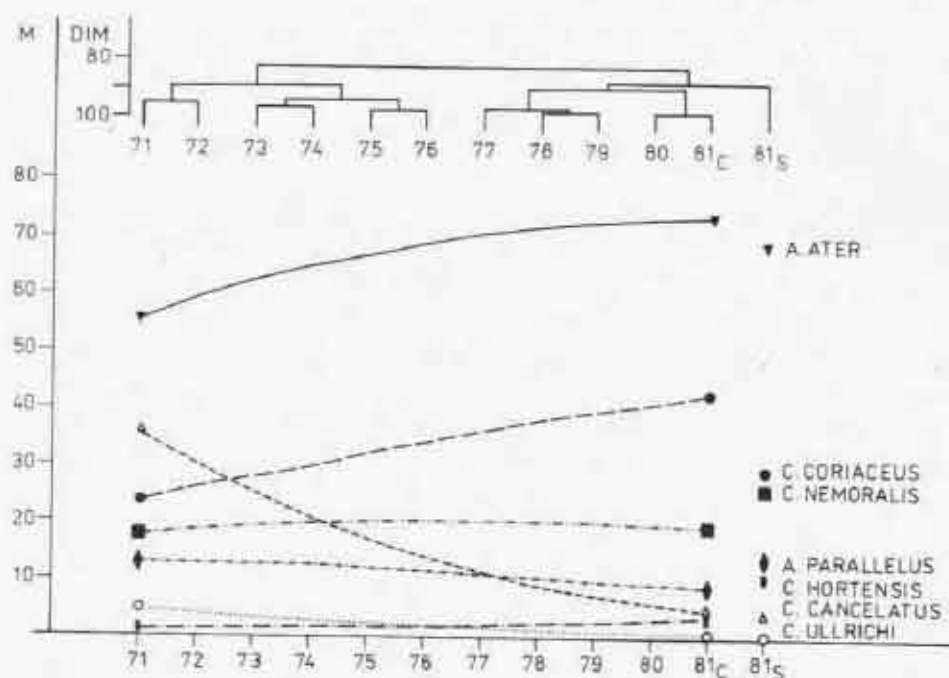


Fig. 46. The prognosis of representation of seven *Carabids* in Fageto Quercetum in Pavlovské kopce hills based on their sex ratios and biomass during 1971 and the comparison of the prognosis with the real sample from 1981 (M ordinate — biomass of individual species in grams, DIM ordinate — dominance identity of biomass in %, abscissa — years, 81_c — predicted community during 1981, 81_s — real community during 1981).

of a taxocenological study, the cluster analysis of dominance identity of biomass of real samples from the years 1971 and 1981 and of the predicted samples from the years 1972, 73, ..., 1981 shows a considerable tendency to form clusters after the subsequent years. One large cluster including the theoretical samples 1972—1976 is formed in the vicinity of real sample from the year 1971, and the second cluster including the theoretical sample from the years 1977—1981 is formed in the vicinity of real sample from the year 1981. The dominance identity of the observed samples from the years 1971 and 1981 is 76.4 %. The identity dominance of

biomass of real sample from 1971 and of theoretical sample from the year 1981 is 74.8 %, and the identity dominance of biomass of the observed and predicted samples from the year 1981 is 86.7 %.

As patent from the above analyses (Fig. 46, Tab. 2), the model makes it possible to estimate the changes in the rank of species in a community with a ten years perspective and to estimate the trend of the changes in the quantitative representation of individual species as well.

Discussion

The different ecological tolerance of both sexes in a species can influence the sexual ratio and it can change the intrinsic growth rate of the population of such species. So, the different ecological tolerance of males and females can be one of causes of a change in the structure of a community. The predominance of females in dominant species in a community exposed to anthropogenous pressure or in a community in less predictable conditions with decisive abiotic regulation coincides well with other characters of these communities such as the low alpha diversity (with some exceptions, of course, Šustek, 1980) or predominance of *r*-selected species, decrease in abundance etc. The increasing predominance of females in disturbed field ecosystems coincides in the time with the increasing trend in representation of smaller species (May 1978 — in relation to latitude, Šustek in press, in relation to anthropogenous influences). A similar coincidence is found also in relation to the simplification of the geographical ranges structure of anthropogenously influenced communities (Šustek, 1980, 1981; Czechowski, 1981; Kubicka, 1981; Cholewicka, 1981) or with the increase in dominance of such species respectively, the range of which have the largest overlap with the range of a biome inhabited by such species (Šustek, 1981). So, the sex ratio of *Carabidae* can be considered as a bioindicative criterium with a high degree of indication ability. The errors of the estimated sex ratio caused by different movability of both sexes can be neglected if the samples obtained by the same collecting method will be used. The influence of the protandry, which is rather frequent in *Carabids* should be eliminated by sampling during a whole season.

The model example shows that the deviations from the normal sex ratio of the species in a community can be used for prognosing of the trend of the development of this community. This mode of the prognosis cannot be, however, used for prognosing the communities in urban ecosystems, profoundly influenced by man, which consist of a large number of immigrants and where the estimated values of the sex ratio can be rather different from the sex ratio of the individuals which really enter the reproduction cycle. This limitation should be applied also on some insular communities surrounded by communities of rather different characters. In such communities, the large portion of migrants is presumable (e. g. Müller, 1970).

Attempts at a prognosis of such communities must be preceded by a profound zoocenological analysis of the communities themselves and of their surrounding.

The proposed model of prognostic application of sex ratio can be used only in groups which have generally more or less balanced sex ratios (the *Carabids* represent such a group). For the groups with obligatory unbalanced sex ratios (e. g. *Sarcophagidae* ♂♂:♀♀=4:1, Povolný, pers. comm.; *Erioccephalidae* ♂♂:♀♀=10:1, Štys, 1981) or for the groups in which their bionomy is responsible for temporal changes in the sex ratio (e. g. *Silphidae*, Špicarová, 1969) the presented prognostic model should be modified specifically.

In the relation to more extensive application of sex ratio in prognosis, the problem of regular cyclic gradations and of the regular changes of sex ratio, known in many pests, must remain open. The knowledge of such phenomena is considerably insufficient in economically indifferent species representing the majority of all animal communities. The probable existence of such cycles suggests the necessity of critical attitude to the proposed mode of prognosis on one hand but it gives a possibility of its specification and, first of all, it indicates the existence of genetic feed-back; and of microevolution offering a chance of survival to species disappearing at present.

Conclusions

1. The sex ratio of *Carabidae* represents an applicable bioindicative criterion of anthropical influence upon the ecosystems. It can be even more indicative than some other criteria due to extensive biological interpretability of sex ratio.

2. The sex ratio of *Carabidae* is applicable also to the approximate prognosis of development in a community exposed to anthropical or abiotical pressures.

3. The bioindicative and prognostic application of sex ratio may be extended also on other groups with obligatory balanced sex ratio and with non-overlapping generations. Their extension on the groups having no above characters is possible only after specific modifications of the presented mathematical model and after a profound study of normal sex ratios in certain groups.

4. The problems of bioindicative and prognostic application of sex ratio of *Carabidae* discussed in the present paper suggest the necessary orientation of zoo-ecological investigations also on long-term changes in animal communities, on the study of population dynamics of species used in the bioindication, and on a more precise typization of animal communities.

Translated by the author

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Šustek Zb.: **Bioindikačný a prognostický význam pomeru pohlaví u bystruškovitých (*Col. Carabidae*).**

Autor sa zaoberá vzťahom pomeru pohlaví u bystruškovitých (*Col. Carabidae*) k poradiu druhu v spoločenstve a k antropogénnemu ovplyvneniu tohto spoločenstva. Rozlišuje päť typov rozdelenia pomeru pohlaví v spoločenstve, ktoré zodpovedajú prirodzeným lesným geobiocenózam v dubovom až dubovo-bukovom vegetačnom stupni, prirodzeným lesným geobiocenózam v bukovom až smrekovo-jedľovo-bukovom vegetačnom stupni, silne ovplyvneným lesným geobiocenoidom v dubovom až dubovo-bukovom vegetačnom stupni, poľným kultúram a izolárnym spoločenstvám vo veľkých mestách a vysvetľuje ich príčiny. V práci sa uvádza približný matematický model, ktorý umožňuje na základe pomeru pohlaví stanoviť odhad trendu ďalšieho vývoja spoločenstva za predpokladu rovnakej intenzity pôsobenia všetkých vonkajších faktorov. Potvrďuje sa možnosť bioindikačného a prognostického využitia pomeru pohlaví bystruškovitých a uvádza niekoľko úvah o možnostiach jeho využitia i u iných skupín živočíchov.

Шустек Зб.: **Биоиндикационное и прогностическое значение соотношения полов у жуков (*Col. Carabidae*).**

Автор занимается отношением соотношения полов у жуков *Col. Carabidae* к очередности вида в сообществе и к антропогенному влиянию на это сообщество. Отличает пять типов разделения соотношения полов в сообществе, которые соответствуют естественным лесным геобиоценозам в дубовой даже буковой вегетационной степени, естественным лесным геобиоценозам в буковой даже елово-пихтово-буковой вегетационной степени, находящимся под сильным влиянием лесного геобиоценоида в дубовой даже дубово-буковой вегетационной степени, полевым культурам и изолированным сообществам в крупных городах и объясняет их причины. В работе предоставляется приближительная математическая модель, которая позволяет на основе соотношения полов установить оценку тренда прогноз дальнейшего развития сообщества при условиях одинаковой интенсивности влияния всех внешних факторов. Подтверждается возможность биоиндикационного и прогностического использования соотношения полов *Col. Carabidae* и проводится несколько рассуждений о возможностях его использования также у других групп животных.