

Peculiarities of Spatial and Temporal Differentiation of Carabids (Coleoptera, Carabidae) in the Steppe Zone

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Abstract—Data on flight phenology of 16 most abundant carabid species in the lower Prut region are provided. Four phenological groups are distinguished. Some species are characterized by constant timing of flight, independent of environmental conditions; the timing of flight in other species is variable and not necessarily the same in different seasons. Some spring-summer and summer-autumn species belong to the second group, whereas spring and autumn species have a more constant timing. Spatial and temporal differentiation of species belonging to the genera *Clivina*, *Stenolophus*, and *Harpalus* (subgenus *Pseudoophonus*) in the steppe zone is discussed. The different timing of maximum flight activity facilitates differentiating closely related species in space and time. Periods of maximum flight activity in the species occupying similar habitats never coincide in time, which results in the most effective resource usage.

Studies of spatial and temporal structure of the populations and species differentiation in communities constitute one of the central problems of modern ecology. The main criterion of spatial differentiation of species is thought to consist in either niche divergence (Gryuntal', 1982; Sowig, 1986; Loreau, 1987; Schultz, Hadely, 1987; Holliday, 1988; Schultz, 1989; Blinshtein and Orlov, 1990; Nazarenko and Chernyakhovskaya, 1990), or temporal differentiation, defined as discrepancy in activity rhythms between the species (Drift, 1959; Williams, 1959; Sota, 1985; Potapova, 1990). The latter is usually limited to discussing the peculiarities of the seasonal or, less frequently, diurnal activity dynamics. The best results can evidently be achieved by considering both spatial and temporal components simultaneously; however, such works are regrettably scarce (Müller, 1985; Andersen, 1988; Gryuntal', 1993).

In almost all investigations of the spatial and temporal population structure dealing with carabids as model objects, the ground activity is primarily considered. This results from ground traps' being the main tool in the monitoring (Prisnyi, 1987; Andersen, 1988; Nazarenko and Chernyakhovskaya, 1990; Budilov, 1992). On the other hand, such methods as window or light traps, reflecting some aspects of the insect flight activity, may also provide good results.

It is known that spatial redistribution of the young imago generation in many Carabidae is accomplished by active flight to a greater extent than by ground mi-

grations (Huizen, 1977; Desender, 1989; Matalin, 1992a). Because of this, data concerning the phenology of flight allow one to time more precisely the periods of activity in imagoes of both sexes at early physiological stages. Subsequently, on the basis of these periods, the number of generations in populations of a certain species during a season can be determined (Bogush, 1951, 1958; Belousov, 1986; Kadar and Lovei, 1987; Karpova and Matalin, 1990). In some cases, the flight phenology data may help to significantly elucidate the spatial and temporal distribution of co-occurring species.

This work is aimed at studying the peculiarities of the spatial and temporal differentiation of closely related carabid species in the steppe zone, with a detailed analysis of the role of the flight migratory activity.

MATERIALS AND METHODS

The material was collected in environs of Roshu settlement (Lower Prut Region, near Kakhul, SW Moldova) in 1990–1991. Data for 1982 from the same locality were kindly provided by V.E. Karpova.

In 1990–1991, carabids were sampled since May till October in 7 natural and 5 agricultural biotopes, using ground, light, and window traps, and also by manual collecting. The ground trap consisted of a glass jar with a volume of 0.5 l and an opening diameter of 72 mm (Barber, 1931). Ten traps were set in each biotope during the vegetation period. The light trap con-

sisted of a "Pennsylvania" light source with a 15W UV lamp (Frost, 1957) and an original collecting device designed by the author (Matalin, 1992). Two light traps were set at permanent sites (in the floodland and above the slope) during the entire investigation period.

The sex and age structure of populations was analyzed using the method proposed by Wallin (1987); 4 physiological age classes were distinguished in imagoes of both sexes (juvenile, immature, generative, and postgenerative). A total of more than 50000 carabid specimens belonging to 257 species were identified and dissected during the investigation. The biotopic distribution of certain species and their relation to the humidity and salinity regime of the soil is characterized using published data (Larsson, 1939; Horion, 1941; Habermann, 1968, Adashkevich, 1972; Petrusenko, 1971; Petrusenko, 1972; Petrusenko, Petrusenko, 1972; Kryzhanovskii, 1983; Rizun, 1991; Hieke and Wrase, 1988; Lindroth, 1992) and the author's observations (Matalin and Karpova, 1991; Karpova and Matalin, 1991, 1993; Matalin, 1993, 1996). Morphometric parameters were measured using a standard eyepiece micrometer and an MBS-1 binocular microscope; values of the standard deviation are provided after \pm sign. The statistical data processing was performed using a "KARAT-M" database management system run on an IBM PC/AT computer. Phenological groups were established by raw data clustering using the "non-weighted mean" method.

RESULTS AND DISCUSSION

Comparison of Carabid Catches in Window and Light Traps in the Steppe Zone

The possibility of using light traps to determine the insect flight activity has been discussed repeatedly (Williams, 1940; Mazokhin-Porshnyakov, 1956; Terskov and Kolomiets, 1966; Chernyshev, 1961; Samkov, 1984, 1984a; Chernyshev *et al.*, 1984; Highland, Lummus, 1986; Allan, 1988; White, 1988, 1989). The flight attracted by artificial light sources undoubtedly constitutes only a part of the total flight activity. However, no method of monitoring flying insects is available that would provide an unambiguous estimation of this activity. Even the most unbiased window traps may give considerably distorted data (Furst and Duelli, 1988; Chernyshev, 1996). When estimating the efficiency of a method, peculiarities of the model insect groups and the natural and climatic conditions of the region in question are to be taken into account as well. In northern and moderate latitudes, light traps have a

restricted use owing to the weather factors (Zhantiev and Chernyshev, 1960; Huizen, 1979; Matalin, 1989); however, in southern regions (steppes and semi-deserts) they provide a vast and representative material during the entire vegetation season (Bogush, 1951; Belousov, 1986; Karpova and Matalin, 1990; Matalin, 1996a).

According to our data, the main abundance peaks of light and window trap catches in the steppe zone partially coincide (Fig. 1A). This is primarily true for early periods, when the initial flight peaks for some species as determined from catches by both trap types almost entirely coincide (Figs. 1B–1C). Later, the effectiveness of window traps decreases, whereas that of light traps continues to rise. This partly agrees with previously obtained data (Samkov, 1984), indicating that the flight period as determined by window traps comes earlier relative to that determined by light traps.

The fact that the initial flight peaks with respect to both trap types considerably coincide in the steppe zone, allows the flight activity of carabids to be estimated with a small error on the basis of light-trapping, regardless of the intrinsic motivation of individuals. In this connection, the "flight migratory activity" will primarily refer to the light-attracted flight; the entire discussion below is based on the data on light trap catches.

Phenology of the Flight Activity in Prevalent Carabid Species in the Steppe Zone

Comparison of flight time and intensity in 16 most prevalent carabid species revealed 4 groups differing in the periods of flight (Fig. 2).

Stenolophus skrimshiranus Steph. and *Acupalpus luteatus* Duft. belong to the species with the spring type of the flight activity; their flight peak is usually observed in the beginning of May–mid-June. In spring-summer species, the increased flight activity occurs in mid-May–mid-July; this group includes *Tachys micros* F.-W., *Stenolophus discophorus* F.-W., *S. mixtus* (Herbst), *S. proximus* Dej., *Clivina ypsilon* Dej., and *Agonum ludens* Duft. The group of species with the summer-autumn flight period includes *Clivina fossor* L., *C. laevifrons* Chaud., *Harpalus (Pseudoophonus) rufipes* (Deg.), and *Anisodactylus signatus* Panz., whose flight activity is at a maximum in the end of June–mid-August. Autumn species, characterized by the maximum flight activity in mid-August–mid-September, include *Harpalus (Pseudoophonus)*

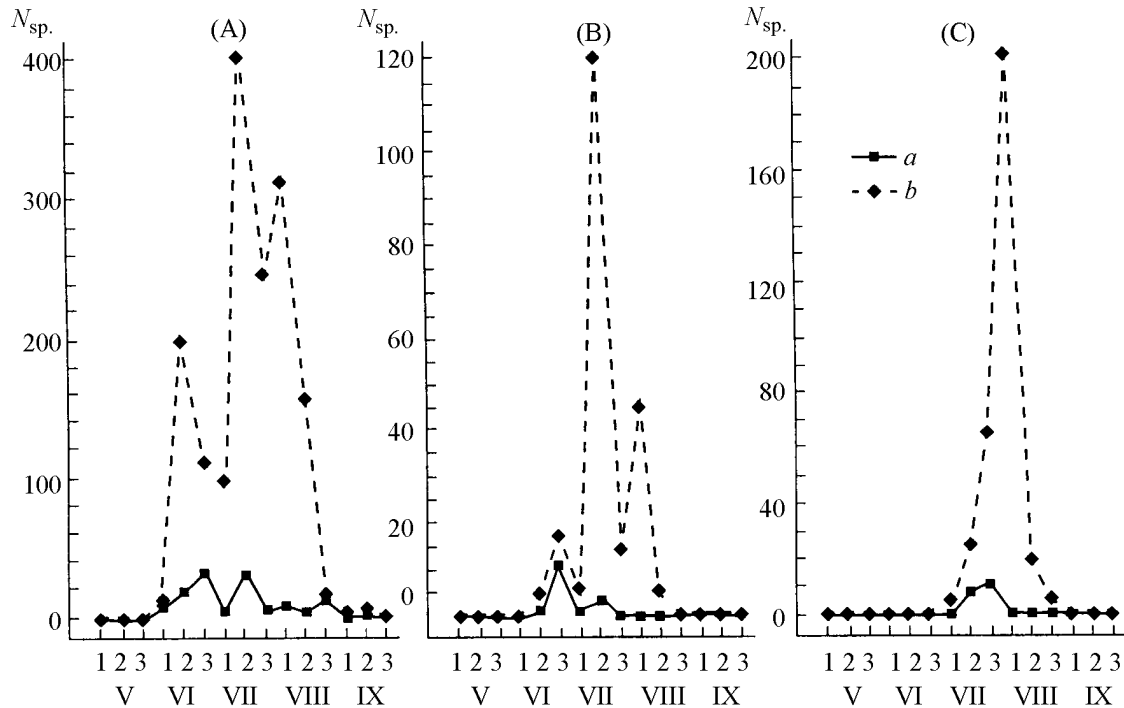


Fig. 1. Ratio of catches by light and window traps in Prut River floodlands in 1991. (A) All Carabidae; (B) *Harpalus (Pseudoophonus) rufipes*; (C) *H. (P.) calceatus* (a—window traps; b—light traps; 1–3, 10-day intervals of a month; V–IX, months).

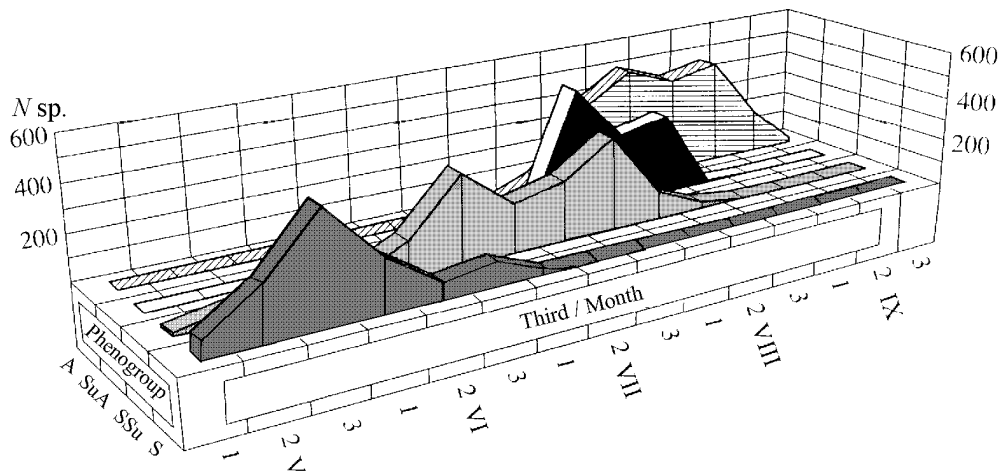


Fig. 2. Seasonal succession of the phenological groups of carabids based on the flight activity of species (average values over the entire study period). S—spring; SSu—spring-summer; SuA—summer-autumn; A—autumn (1–3, 10-day intervals of a month; V–IX, months).

calceatus Duft., *H. (P.) griseus* Panz., *Amara apricaria* Payk., and *Curtonotus convexiusculus* Marsh. (Figs. 3, 4).

Although the maximum flight periods are generally rather clearly delimited, some carabid species may fit into different groups in different seasons, with the maximum flight shifted to earlier or later periods. For example, in the dry year of 1990, the flight activity in a summer-autumn species, *C. fossor*, shifted to an earlier period, as a result of which the species was characterized as a spring-summer one. Similarly, a

spring-summer species, *C. ypsilon*, fell into the spring group in 1990. In the abnormally rainy year of 1991, *T. micros* displayed flight activity in spring, whereas the species normally belongs to the spring-summer group. On the contrary, the maximum flight activity in *S. proximus* shifted to a later period in 1991, so that the species was characterized as a summer-autumn one, though it is usually active in spring-summer (Figs. 3, 4).

Thus, groups with spring-summer and summer-autumn flight periods display varied degree of stability

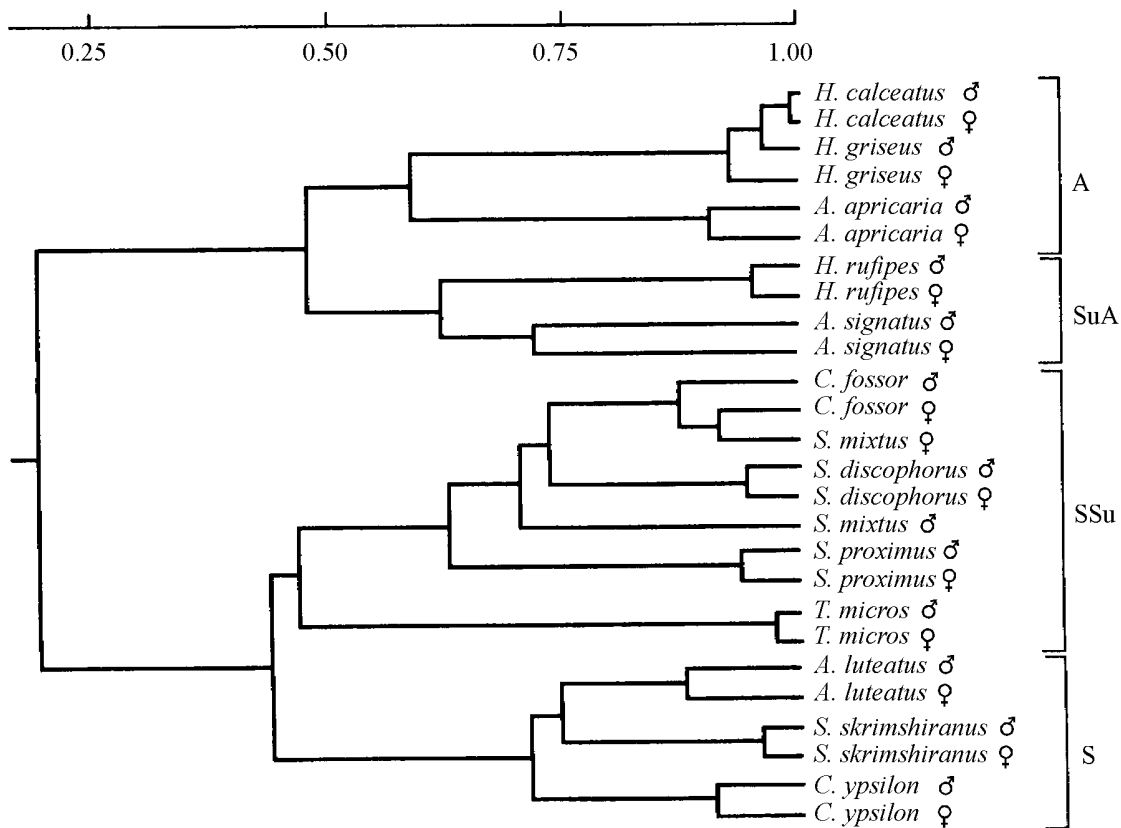


Fig. 3. Degree of similarity and species composition of the phenological groups of carabids based on light-trapping in 1990. S—spring; SSu—spring-summer; SuA—summer-autumn; A—autumn.

of flight peak terms over the season. Some species (termed obligatory species) are characterized by constant flight periods under changing environmental conditions, owing to a high flight activity in all physiological stages of the imago. Other (facultative) species are rather labile in that their flight periods vary over seasons. In spring species, the constant flight periods are related to the ephemeral life cycles, with generative and postgenerative individuals dying almost immediately after reproduction. In autumn species, the stable flight periods result from limitations caused by weather conditions and also by wing musculature autolysis in later stages of the life cycle.

It is worth noting that congeneric species often belong to different phenological groups, which indicates a considerable divergence in their seasonal activity. Such data, representing an important ecological feature, are of indubitable interest for understanding the ways of differentiation of co-occurring species.

Role of the Flight Migratory Activity in the Spatial and Temporal Differentiation of Closely Related Carabid Species

The most complete data sets concerning the flight periods as determined by light-trapping, the distribu-

tion over biotopes, and relation to the humidity and salinity regime of the soil have been obtained for species belonging to the genera *Clivina* and *Stenolophus* and the subgenus *Pseudoophonus* (genus *Harpalus*). Each taxon has a peculiar type of spatial and temporal differentiation of closely related species.

Species of *Clivina* have one of the simplest types. Of the 4 species belonging to this genus (*C. fossor*, *C. ypsilon*, *C. laevifrons*, and *C. collaris*), the first 3 are most abundant in the area studied. They belong to the same life form (burrowing geobionts) and have about the same size (6.21 ± 0.12 mm, 6.57 ± 0.18 mm, and 5.25 ± 0.1 mm, respectively), resulting in a considerable similarity of the occupied ecological niches. The probability of interspecific competition is very high in the co-occurring species; in this case, generative females may compete for the most convenient places of reproduction, and juveniles and generatives of either sex, for food, because at these particular stages the carabids are most sensitive to food deficiency (Müller, 1985; Pearson and Knisley, 1985).

The competition is partly reduced due to different relation of these species to the humidity and salinity regime of the soil and the resulting spatial differentia-

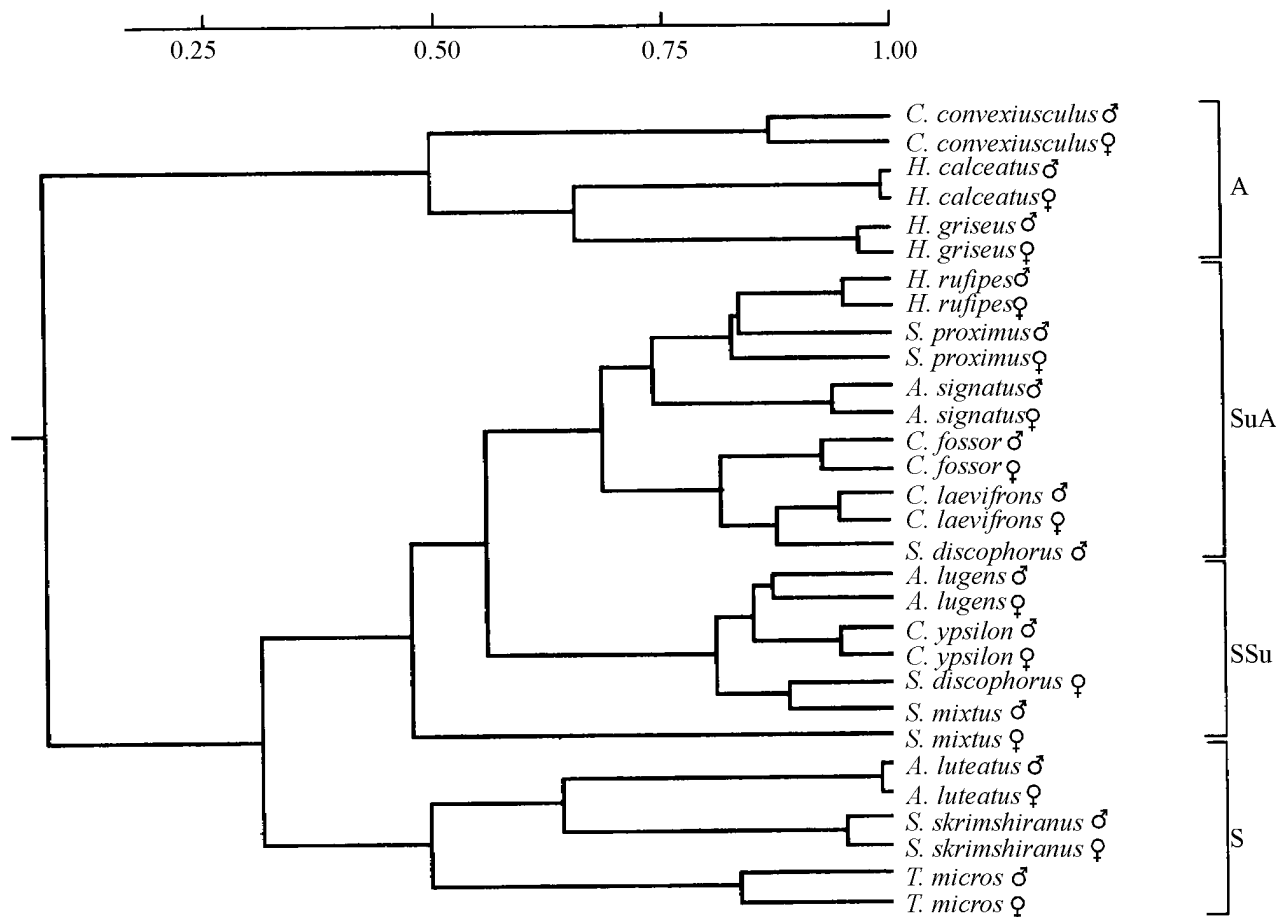


Fig. 4. Degree of similarity and species composition of the phenological groups of carabids based on light-trapping in 1991. Legends as in Fig. 3.

tion. *C. ypsilon* and *C. laevifrons* are rather tolerant to saline soils and often found on humid saline soils and salt marshes, whereas *C. fossor* cannot tolerate any degree of salification at all (Horion, 1941; Petrusenko, 1971; Petrusenko, 1972; Kryzhanovskii, 1983; Karpova, 1986; Utyanskaya, 1986; Hieke and Wrase, 1988). However, the inhabited stations of *C. ypsilon* and *C. laevifrons* considerably overlap. In those cases when these species co-occur, the terms of emergence and maximal flight (dispersion) of the young beetle generation do not coincide. For example, the maximal flight as determined by light-trapping occurs in the middle third of June in *C. ypsilon*, and in the middle third of July in *C. laevifrons* (Fig. 5). This allows more effective use of food and micro-statal recourses of the biotopes. Müller (1987) and Sota (1985) discuss the different emergence periods in similar-sized carabid species as a possible way of reducing the competition for food recourses.

Species of the subgenus *Pseudoophonus* (genus *Harpalus*) display a similar, though more complicated

variant; this variant is of the greatest interest, since these species are most abundant in various agrocenoses of almost every zone in Europe (Larsson, 1939; Briggs, 1965; Luff, 1978; Sharova, 1990). A considerable amount of data concerning their spatial differentiation has been obtained. In particular, different natural and climatic zones have distinctly different dominant species. For example, *H. (P.) griseus* Panz. is the most abundant species in the forest-steppe agrocenoses (Kasandrova, 1970; Popova, 1986; Kasandrova and Romankina, 1991); *H. (P.) rufipes* Deg. dominates in irrigated steppes (Karpova, 1986; Nazarenko, 1990; Matalin, 1993); whereas *H. (P.) calceatus* is the most abundant species in dry steppes and semi-deserts (Sharova and Lapshin, 1971; Potapova, 1972; Utyanskaya, 1986; Cherezova, 1990).

Species of this genus are also characterized by biotopic preferences with regard to the general humidity regime within the same natural and climatic zone. For example, according to Saipulaeva (1990), *H. (P.) calceatus* is dominant in non-irrigated orchards in

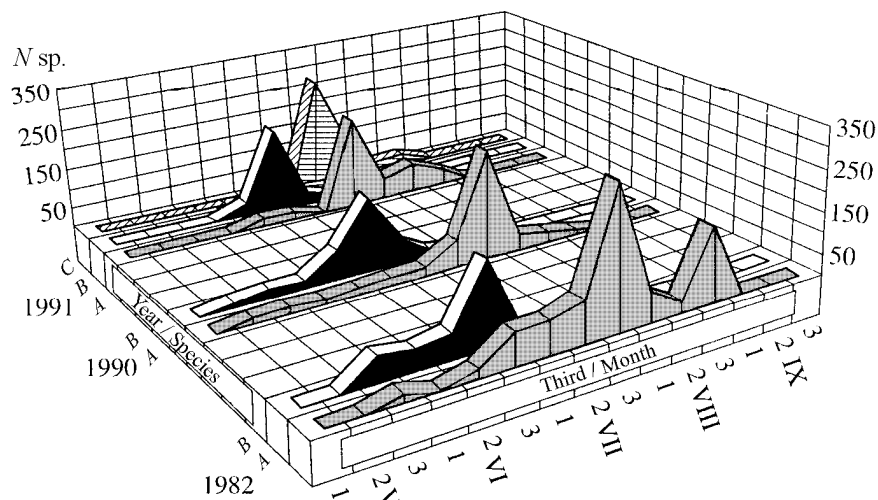


Fig. 5. Seasonal flight dynamics determined by light-trapping in species of the genus *Clivina*. (A) *C. fossor*; (B) *C. ypsilon*; (C) *C. laevifrons* (1–3, 10-day intervals of a month; V–IX, months).

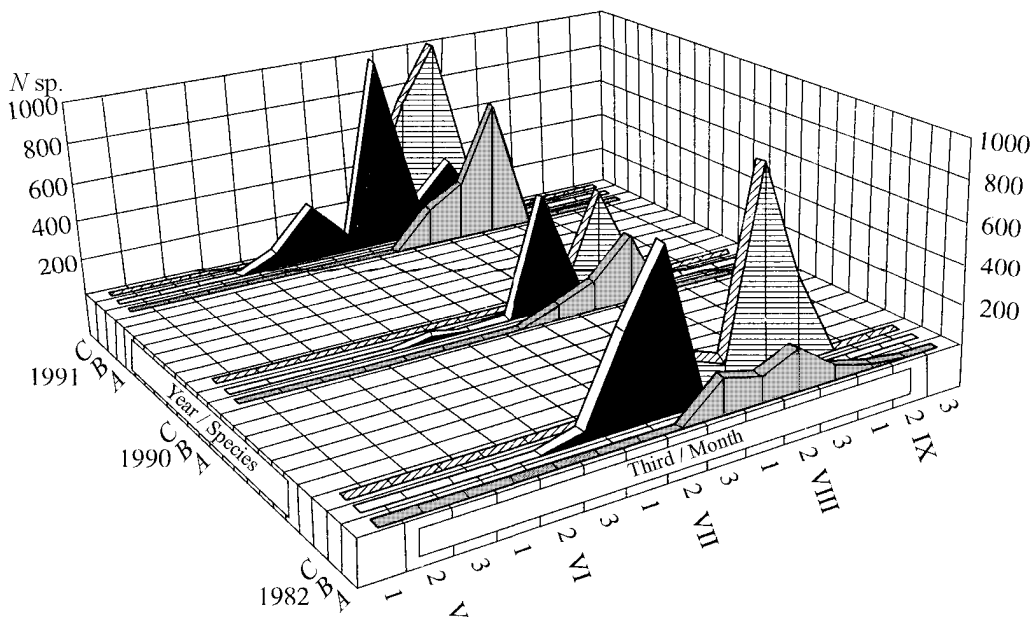


Fig. 6. Seasonal flight dynamics determined by light-trapping in species of the subgenus *Pseudoophonus* (genus *Harpalus*). (A) *H. griseus*; (B) *H. rufipes*; (C) *H. calceatus* (1–3, 10-day intervals of a month; V–IX, months).

Dagestan and clearly prefers drier biotopes, thus differing from *H. (P.) rufipes* and *H. (P.) griseus*. according to Karpova (1986) and the author's observations (Matalin, 1993); in SW Moldova *H. (P.) calceatus* prefers xerophytic floodland landscapes of large river terraces, where its abundance is high. On the contrary, *H. (P.) rufipes* and *H. (P.) griseus* prefer more mesophytic, and the latter, even hygrophytic floodland landscapes. Haas (1988) mentions that in

S Tyrol, *H. (P.) calceatus* is more xerophytic than other congeneric species.

Thus, the co-occurring species of the subgenus *Pseudoophonus* are spatially differentiated on the basis of a different relation to the general soil humidity regime. However, as in the previous case, the spatial differentiation does not provide complete separation. In particular, the niches of *H. (P.) rufipes* and

Micro-statal distribution of *Stenolophus* species (%) near Fundul-Roshu spring: data obtained using ground traps and manual collecting, 1990

Species	Near water						Far from water
	open areas					under tree cover	
	raft and ligneous litter	sparse herb vegetation	bulrush on dark clay soil	sedge and rush tussocks	thick grass vegetation	thick herb vegetation	sparse herb vegetation and ligneous litter
<i>S. discophorus</i>	14.0	5.5		5.0	50.0	5.0	4.0
<i>S. persicus</i>	32.0	26.0	8.0	38.0	7.0		15.5
<i>S. teutonius</i>	11.5	31.5		12.0	6.0		5.5
<i>S. mixtus</i>	18.0	21.0	23.0	14.0	26.0	5.0	70.0
<i>S. proximus</i>	7.5	5.0	69.0	2.0	1.5		
<i>S. skrimshiranus</i>	17.0	11.0		29.0	9.5	5.0	5.0
<i>S. steveni</i>						85.0	

H. (P.) griseus noticeably overlap owing to a similar size (14.06 ± 1.93 mm and 10.48 ± 0.83 mm, respectively) and the same diet (Gersdorf, 1937; Sharova, 1981). The temporal differentiation of these species, resulting from different terms of emergence, and subsequent dispersion and reproduction of the young imago generation, proves to be the most effective. In the steppe zone, the flight peak of *H. (P.) rufipes* occurs in the middle third of July, and of *H. (P.) griseus*, in the middle third of August (Fig. 6). It is interesting that in Hungary the flight peak of the latter species (as determined by light-trapping) is also observed in mid-August (Kadar and Lovei, 1987).

The most complicated variant of escaping the interspecific competition is demonstrated by species of the genus *Stenolophus*, owing to the fact that in the area studied, a large number of species may inhabit the same biotope. For example, the carabid community of the Fundul-Roshu spring (2 km N of Roshu settlement) included 7 species, co-occurring along a 100–120 m long segment of the spring (table). This indicates that their spatial and temporal differentiation is effective. The most complete data on the seasonal activity dynamics were obtained for 4 species: *S. mixtus*, *S. discophorus*, *S. skrimshiranus*, and *S. proximus*.

The *Stenolophus* species are hygrophiles inhabiting different near-water biotopes. As in *Clivina* species, the spatial differentiation results from the different

relation to the humidity and salinity regime of the soil. According to published data (Horion, 1941; Hieke and Wrase, 1988) and the author's observations (Matalin, 1996), *S. proximus* differs from its congeners in preferring the dense dark-clay, semi-saline or saline soils (table). The temporal differentiation results from different terms of the young imago flight peak in *S. skrimshiranus* (middle third of May–middle third of June), on the one hand, and in *S. discophorus* and *S. mixtus* (middle third of July), on the other (Fig. 7). At the same time, *S. discophorus* and *S. mixtus*, being the most abundant species in the area studied, have similar distribution and terms of flight. Although *S. discophorus* prefers to a greater extent bogged meadows and areas of thick grass vegetation, it gains no significant advantage, because *S. mixtus*, being the most eurytopic species, also may be very abundant in these biotopes (table). These species have a largely similar size (5.8 ± 0.2 mm in *S. mixtus* and 6.4 ± 0.51 mm in *S. discophorus*) and diet (author's observations), which lessens the possibility of trophic isolation. According to the data obtained, light traps collect mainly females in *S. mixtus*, but males in *S. discophorus* (Fig. 8). It is probable that the isolation in this case results from different behavioral strategies of sexes.

In our opinion, in the first case, females of *S. mixtus* follow the territorial expansion strategy aimed at finding suitable places for oviposition. Such an ap-

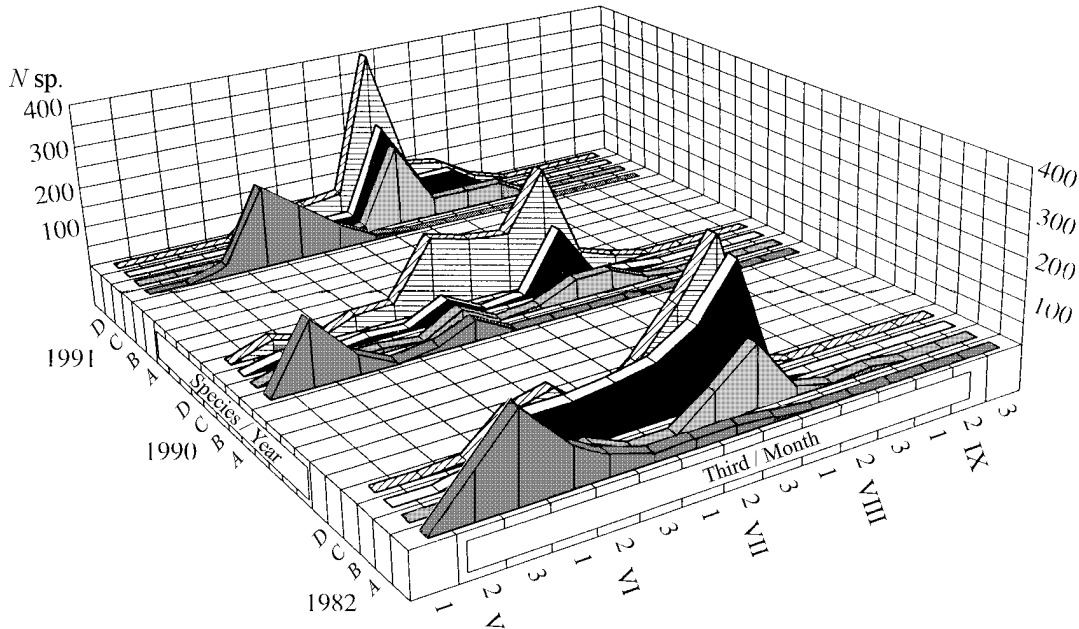


Fig. 7. Seasonal flight dynamics determined by light-trapping in species of the genus *Stenolophus*. (A) *S. skrimshiranus*; (B) *S. proximus*; (C) *S. mixtus*; (D) *S. discophorus* (1–3, 10-day intervals of a month; V–IX, months).

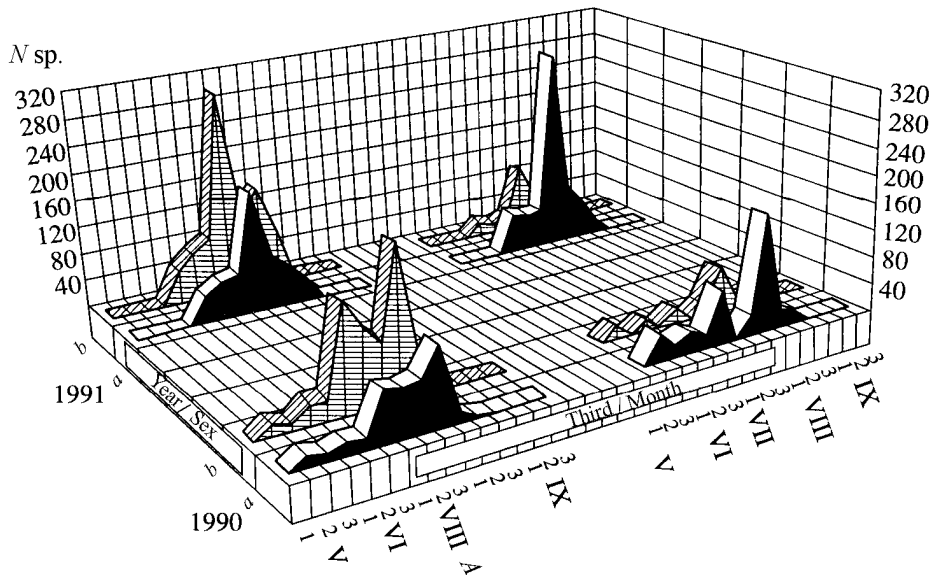


Fig. 8. Seasonal flight dynamics determined by light-trapping in different sexes of *S. mixtus* and *S. discophorus*. (A) *S. discophorus*; (B) *S. mixtus*; (a) females; (b) males (1–3, 10-day intervals of a month; V–IX, months).

proach may be termed the “intensive” one: every season, the females are redistributed over new territories, thus facilitating not only survival of the species, but also its considerable abundance.

The second case most probably represents the active mate search by males. It is possible that females of

S. discophorus are less active prior to copulation. However, the potential flight distances do not differ significantly between males and females of this species (Matalin, 1992a). Here, the “extensive” approach is most likely to occur: the redistribution of the species is accomplished mostly by the higher activity of males, whereas females remain within some restricted area,

using its resources. This may result from the fact that *S. discophorus* is relatively stenotopic as compared to *S. mixtus*.

The obtained data indicate that closely related carabid species demonstrate different variants of interspecific isolation based on spatial and temporal differentiation. In a number of cases, the species prefer biotopes and micro-stations with rather strictly determined living conditions. In other cases, species are differentiated owing to different terms of their maximal flight (this being an example of different seasonal activity patterns). The maximal flight activity periods in closely related species occupying similar habitats almost never coincide. This allows such species to use the resources most effectively. When the specific diversity of a genus in the community is the highest, the most complicated variants of differentiation are observed. Complex spatial (habitat preferences) and temporal (different terms of imago activity) differentiation facilitates the maximal separation of species and reduces the interspecific competition to a minimum.

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