

Daily activity of carabid beetles (Coleoptera: Carabidae) in the forests of various geographical zones in the East European (Russian) plain

Суточная активность жужелиц (Coleoptera: Carabidae) в лесах разных географических зон Восточно-Европейской равнины

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КЛЮЧЕВЫЕ СЛОВА: Coleoptera, Carabidae, суточная активность, леса, Восточно-Европейская (Русская) равнина.

ABSTRACT. The studies were carried out in forests of the middle taiga, in the mixed forest zone and in the forest-steppe. For each geographical zone typical forests were chosen. The beetles were trapped using pitfall traps without fixative, which were controlled twice a day. In the latter case they were checked before sunset and immediately after sunrise. The results demonstrate, that carabids in the middle taiga as well as in forest-steppe are characterised by diurnal activity, but in the mixed forest zone by nocturnal activity. The peculiarities of daily activity of the dominant species are analysed in detail.

РЕЗЮМЕ. В лесостепи, а также в средней тайге и зоне смешанных лесов изучали суточную активность жужелиц. Для учёта жуков использовались ловушки без фиксатора, выборка которых осуществлялась дважды в сутки (перед заходом и сразу после восхода солнца). Установлено, что в средней тайге и лесостепи у жужелиц преобладает дневная активность, тогда как в зоне смешанных лесов — ночная. Обсуждаются особенности суточной активности доминантных видов.

Introduction

Analysing the daily activity of carabid beetles in one branch concerning studies of the ecology of these insects. Informations about the pattern of daily activity of 67 middle european carabid species are summarised by Thiele [1977]. The list of species is constantly replenished because of the studies both of russian [Shilenkov, 1978; Gryuntal, 1981, 1988a; etc.] and foreign specialists [Schiller & Weber, 1975; Stubbe et al., 1984; etc.], but all the mentioned studies were carried out only one geographical zone.

Material and methods

The given paper presents a comparative study of the daily activity of carabid beetles in the forests of three zones of Russian plain: in the boreal forests (more precisely in the middle taiga), in mixed forests (in broad-leaved spruce forests) and in forest-steppe.

All studies were carried out with standard methods. In each forest type 60–80 pitfall traps (glass jars of 0.5 l capacity, 72 mm upper diameter) without fixative were arranged in one line with a distance of five meters from each other. To win informations about the distribution of the activity over light and dark periods of the day the pitfall traps were checked twice a day: before sunset and immediately after sunrise. To study the distribution of activity during daylight traps were checked every hour. The captured carabids were determined directly in the field and set free after this procedure with exception of the larvae (their determination under field conditions is rather complicated). Daily activity was studied over the period of 4–6 days (without precipitation) during the periods of maximum activity of the beetles. The following formula was used to estimate significance of differences between the activity during light and dark periods of the day: $\chi^2 = \Sigma (a - b)^2 / b$; with: a — actually observed number of specimens, b — their theoretically expected number.

Studies in the middle taiga were carried out near Gribanikha village (Onezhsky district of Arkhangelskaja region) in 1990–1991. The carabids were captured in *Tremuleto-megaherboso-oxalidosum* (55–60 years old) at the end of June and beginning of August. According to our studies this period is marked by the maximum seasonal activity of these beetles. Overall during the period of study about 1000 individuals of adults belonging to 10 species were captured (Tab. 1).

Table 1. Daily activity of carabid beetles in Tremuleetum megaherboso-dryopteridoso-oxalidosum (Arkhangelskaja region, middle taiga).
Таблица 1. Суточная активность жужелиц в Tremuleetum megaherboso-dryopteridoso-oxalidosum (Архангельская область, средняя тайга).

Species	June				August				Total for biotope			
	Day	Night	% of day activity	χ^2	Day	Night	% of day activity	χ^2	Day	Night	% of day activity	χ^2
<i>N. big.</i>	10	—	100.0	5.0	2	—	100.0	1.0*	12	—	100.0	6.0
<i>L. pil.</i>	11	2	84.6	6.2	1	1	—	—	12	3	80.0	24.3
<i>T. sec.</i>	—	—	—	—	370	156	70.3	87.1	370	156	70.3	87.1
<i>B. man.</i>	9	4	69.2	1.9*	—	—	—	—	9	4	69.2	1.9*
<i>B. bul.</i>	10	—	100.0	5.0	1	2	—	—	11	2	84.6	6.2
<i>P. atr.</i>	58	32	64.4	7.51	32	37	46.4	0.4*	90	69	56.6	2.8*
<i>P. obl.</i>	27	11	71.0	6.74	2	2	—	—	23	13	63.9	6.1
<i>P. mel.</i>	89	23	79.5	38.9	3	1	—	—	92	24	79.3	39.9
<i>P. str.</i>	15	9	62.5	1.5*	3	1	—	—	18	10	64.3	3.6*
<i>C. micr.</i>	11	9	55.0	0.2*	—	9	100.0	4.5	11	18	37.9	1.7*
Total	240	90	72.4	68.2	414	209	66.4	67.5	648	299	68.4	132.8

Species are mentioned by their abbreviations: *N. big.* = *Notiophilus biguttatus* F.; *L. pil.* = *Loricera pilicornis* F.; *T. sec.* = *Trechus secalis* Pk.; *B. man.* = *Bembidion mannerheimi* Chd.; *B. bul.* = *Badister bullatus* F.; *P. atr.* = *Patrobus atrorufus* Ström; *P. obl.* = *P. oblongopunctatus* F.; *P. mel.* = *P. melanarius* Ill.; *P. str.* = *P. strenuus* Pz.; *C. micr.* = *Calathus micropterus* Duft.; * — differences statistically not significant.

Виды перечислены в соответствии следующей аббревиатурой: *N. big.* = *Notiophilus biguttatus* F.; *L. pil.* = *Loricera pilicornis* F.; *T. sec.* = *Trechus secalis* Pk.; *B. man.* = *Bembidion mannerheimi* Chd.; *B. bul.* = *Badister bullatus* F.; *P. atr.* = *Patrobus atrorufus* Ström; *P. obl.* = *P. oblongopunctatus* F.; *P. mel.* = *P. melanarius* Ill.; *P. str.* = *P. strenuus* Pz.; *C. micr.* = *Calathus micropterus* Duft.; * — различия статистически недостоверны.

The material in the mixed forest zone was collected at Malinskoje forestry (Podolsky district of Moscow region) in Betuleetum pilosae caricosum (the age of birch was 55–60 years) and in Piceetum coryloso-ruboso-oxalidosum (the age of spruce was about 100 years) in 1979, 1980 and 1985. Carabids were caught from the end May to the beginning of June and from the end July to the beginning of August. These are the periods of their maximum seasonal activity in this region [Gryuntal, 1988b]. About 2700 specimens belonging to 15 species were examined (Tabs 2–3, Fig. 3).

In the forest-steppe the material was collected at Tellermanovskoye experimental forestry (Gribanovsky district of Voronezh region) in 1987, 1988 and 1990. Carabids were collected in the most typical type of forest in this zone, which is the Fraxineto-Quercetum pilosae-caricoso-aegopodiosum (the age of *Quercus* was about 100 years), at the period of maximum activity in this region. According to our observations this period ranges from the end of May to the beginning of June (only one peak of maximum was observed for this region). Moreover, in the middle of July in 1990 material was collected over the period of two days in Quercetum convallarioso-rubosum (the age of *Quercus* was about 100 years) located at the flood plain of Khoper river. In the Fraxineto-Quercetum pilosae-caricoso-aegopodiosum about 1100 specimens belonging to 8 species (Tab. 4) and in the Quercetum convallarioso-rubosum about 63 specimens belonging to six species were collected.

Results

The analysis of the carabids caught in the taiga showed that daily activity prevailed considering the whole time of

study (differences are significant with $p > 0.01$) as well as considering only the maxima of activity.

Three groups of species may be distinguished according to their activity during the day (Tab. 1). The first one is build of the species *Badister bullatus*, *Loricera pilicornis*, *Pterostichus melanarius*, *P. oblongopunctatus* and *Trechus secalis*. These species were active mainly during the day time. Four species (*Bembidion mannerheimi*, *Patrobus atrorufus*, *Pterostichus strenuus*, *Calathus micropterus*) were indifferent they showed no preference to a special period of the day. Finally, *Notiophilus biguttatus* was active exclusively at day time.

Two species — *P. atrorufus* and *C. micropterus*, were rather numerous both in June and August (Tab. 1). It was possible to track their daily activity within these two month. Diurnal activity predominated in *P. atrorufus* in June whereas in August this species showed an indifferent behaviour. *Calathus micropterus* was indifferent in June, but in August all individuals of this species were caught in the night (Tab. 1).

In the period of “white nights” in June, when the pitfall traps were controlled every hour, several peaks of activity were registered during the day (Fig. 1). The highest peak occurred between 21 and 23 p.m. — an hour before and an hour after sunset.

The analysis of the carabid communities showed that — considering all data — activity during the night is dominant in the mixed zone with 57.4% ($\chi^2 = 58.7$). But the most frequent species collected in that two biotopes may be divided into three groups according to their pattern of activity (Fig. 2). The majority of them (six out of eleven species) were active mainly at night. *Pterostichus niger*, *P. melanarius* and *P. aethiops* showed an indifferent behaviour, only two species

Table 2. Daily activity of carabid beetles in *Betuletum pilosae caricosum* in mixed forest zone (Moscow region).
Таблица 2. Суточная активность жужелиц в *Betuletum pilosae caricosum*, зона смешанных лесов (Московская область).

Species	<i>Betuletum pilosae caricosum</i>											
	Spring				Summer				Total for biotope			
	Day	Night	% of day activity	χ^2	Day	Night	% of day activity	χ^2	Day	Night	% of day activity	χ^2
<i>C. gr.</i>	—	5	100.0	2.5*	—	1	—	—	—	6	100.0	3.0*
<i>L. ter.</i>	—	—	—	—	2	5	28.6	1.28*	2	5	28.6	1.28*
<i>L. pil.</i>	8	4	66.7	1.3*	43	8	84.3	24.0	51	12	81.0	24.1
<i>T. sec.</i>	—	—	—	—	107	75	58.8	5.6	107	75	58.8	5.6
<i>P. atr.</i>	—	—	—	—	81	337	19.4	156.8	81	337	19.4	156.8
<i>P. nig.</i>	1	—	—	—	10	6	62.5	1.0*	11	6	64.7	1.92*
<i>P. mel.</i>	8	38	17.4	19.6	57	15	79.2	24.5	65	53	55.1	1.22*
<i>P. aeth.</i>	4	11	26.7	3.3*	6	5	54.6	0.09*	10	16	38.5	1.38*
<i>P. ass.</i>	7	133	5.0	113.4	—	3	—	—	7	136	4.9	116.4
Total	28	191	12.8	121.3	306	455	40.2	29.2	334	646	34.1	99.3

Species are mentioned by their abbreviations: *C. gr.* = *Carabus granulatus* L.; *L. ter.* = *Leistus terminatus* Hell.; *L. pil.* = *Loricera pilicornis* F.; *T. sec.* = *Trechus secalis* Pk.; *P. atr.* = *Patrobus atrorufus* Ström; *P. nig.* = *Pterostichus niger* Schall.; *P. mel.* = *Pterostichus melanarius* Ill.; *P. aeth.* = *Pterostichus aethiops* Pz.; *P. ass.* = *Platynus assimilis* Pk.; * — differences statistically not significant.

Виды перечислены в соответствии следующей аббревиатурой: *C. gr.* = *Carabus granulatus* L.; *L. ter.* = *L. terminatus* Hell.; *L. pil.* = *Loricera pilicornis* F.; *T. sec.* = *Trechus secalis* Pk.; *P. atr.* = *Patrobus atrorufus* Ström; *P. nig.* = *Pterostichus niger* Schall.; *P. mel.* = *Pterostichus melanarius* Ill.; *P. aeth.* = *Pterostichus aethiops* Pz.; *P. ass.* = *Platynus assimilis* Pk.; * — различия статистически недостоверны.

Table 3. Daily activity of carabid beetles in *Piceetum coryloso-ruboso-oxalidosum* in mixed forest zone (Moscow region).
Таблица 3. Суточная активность жужелиц в *Piceetum coryloso-ruboso-oxalidosum*, зона смешанных лесов (Московская область).

Species	<i>Piceetum coryloso-ruboso-oxalidosum</i>											
	Spring				Summer				Total for biotope			
	Day	Night	% of day activity	χ^2	Day	Night	% of day activity	χ^2	Day	Night	% of day activity	χ^2
<i>C. car.</i>	1	—	—	—	1	12	7.7	9.3	2	12	14.3	7.1
<i>C. gr.</i>	16	45	26.2	23.8	1	—	—	—	17	45	27.4	12.6
<i>C. gl.</i>	—	1	—	—	2	6	25.0	2.0*	2	7	22.2	2.8*
<i>L. ter.</i>	—	—	—	—	1	8	11.1	5.4	1	8	11.1	5.4
<i>L. pil.</i>	1	3	—	—	23	6	79.3	10.0	24	9	72.7	6.8
<i>T. sec.</i>	—	—	—	—	380	245	60.8	29.2	380	245	60.8	29.2
<i>P. atr.</i>	12	36	25.0	12.0	128	194	39.8	13.5	140	130	51.8	0.4*
<i>P. nig.</i>	2	—	—	—	11	19	36.7	2.9*	13	19	40.6	1.1*
<i>P. obl.</i>	90	143	38.6	12.1	9	2	81.8	4.4	99	145	40.6	8.7
<i>P. mel.</i>	3	22	12.0	14.4	54	16	77.1	20.6	57	38	60.0	3.8*
<i>P. aeth.</i>	7	29	19.4	13.4	11	3	78.6	4.6	18	32	36.0	3.9
<i>P. ass.</i>	31	179	14.8	104.3	—	1	—	—	31	180	14.7	105.2
<i>A. ful.</i>	—	1	—	—	9	4	69.2	1.9*	9	5	64.3	1.1*
<i>C. mic.</i>	2	1	—	—	2	4	33.3	0.7*	4	5	44.4	0.1*
Total	165	460	26.4	139.2	632	520	54.9	10.9	797	880	47.5	4.1

Species are mentioned by their abbreviations: *C. car.* = *Cychrus caraboides*; *C. gr.* = *Carabus granulatus* L.; *C. gl.* = *Carabus glabratus* Pk.; *L. ter.* = *Leistus terminatus* Hell.; *L. pil.* = *Loricera pilicornis* F.; *T. sec.* = *Trechus secalis* Pk.; *P. atr.* = *Patrobus atrorufus* Ström; *P. nig.* = *Pterostichus niger* Schall.; *P. obl.* = *Pterostichus oblongopunctatus* F.; *P. mel.* = *Pterostichus melanarius* Ill.; *P. aeth.* = *Pterostichus aethiops* Pz.; *P. ass.* = *Platynus assimilis* Pk.; *A. ful.* = *Agonum fuliginosum* Pz.; *C. mic.* = *Calathus micropterus* Duft.; * — differences statistically not significant.

Виды перечислены в соответствии следующей аббревиатурой: *C. car.* = *Cychrus caraboides*; *C. gr.* = *Carabus granulatus* L.; *C. gl.* = *Carabus glabratus* Pk.; *L. ter.* = *Leistus terminatus* Hell.; *L. pil.* = *Loricera pilicornis* F.; *T. sec.* = *Trechus secalis* Pk.; *P. atr.* = *Patrobus atrorufus* Ström; *P. nig.* = *Pterostichus niger* Schall.; *P. obl.* = *Pterostichus oblongopunctatus* F.; *P. mel.* = *Pterostichus melanarius* Ill.; *P. aeth.* = *Pterostichus aethiops* Pz.; *P. ass.* = *Platynus assimilis* Pk.; *A. ful.* = *Agonum fuliginosum* Pz.; *C. mic.* = *Calathus micropterus* Duft.; * — различия статистически недостоверны.

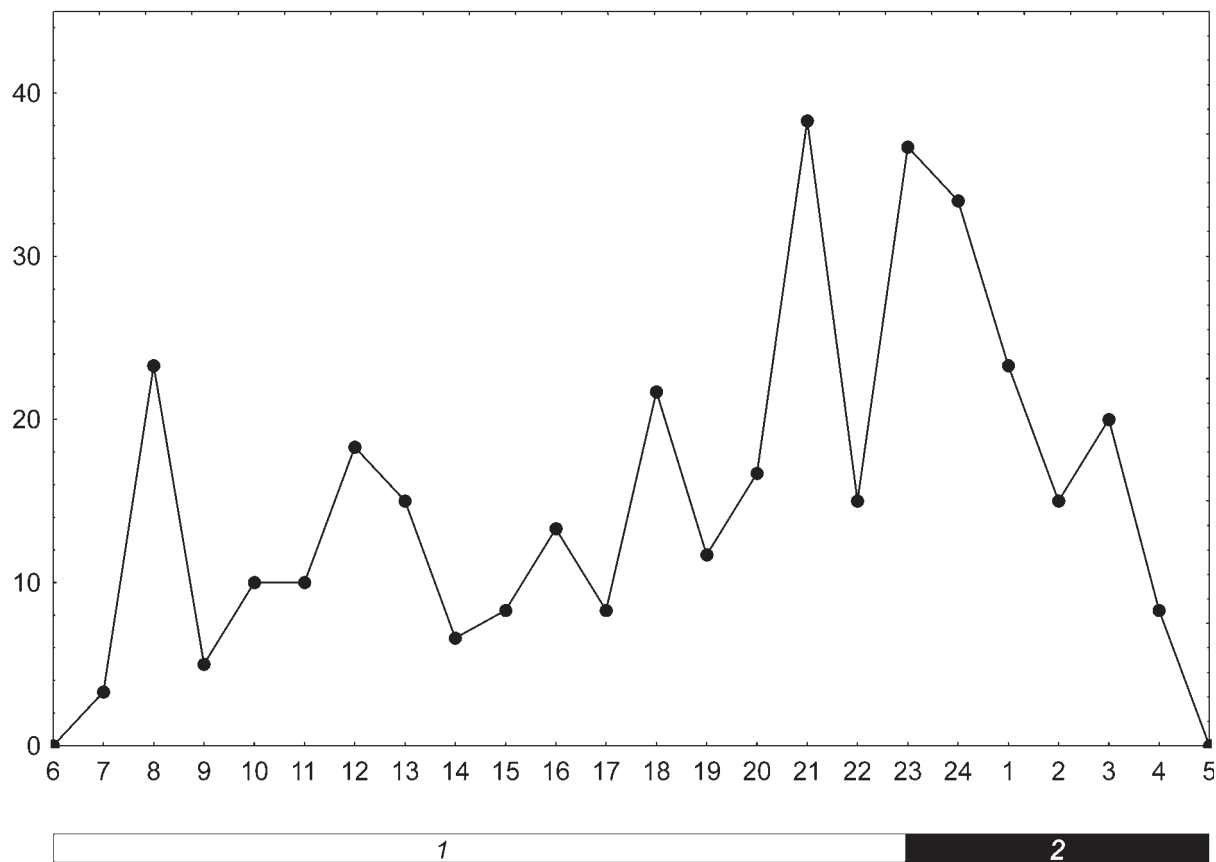


Fig. 1. Daily dynamics of activity of carabid beetles in Tremuleetum megaherboso-dryopteridioso-oxalidosum (middle taiga). White rectangle day; black rectangle – night.

Рис. 1. Динамика суточной активности жужелиц в Tremuleetum megaherboso-dryopteridioso-oxalidosum (средняя тайга). Белый прямоугольник – день; чёрный прямоугольник – ночь.

(*L. pilicornis* and *T. secalis*) were active chiefly at day time (Fig. 2). Due to the fact that the pattern of daily activity of a community is in general defined to great extent by the most frequent species we examined more precisely the distribution of their daily activity in each of the studied forest types. We set our focus on the whole time of the study as well as on the periods of maximum activity of the beetles.

The results demonstrate that activity at night prevailed in average in the Betuleetum pilosae caricosum as well as the Piceetum coryloso-ruboso-oxalidosum (Tabs 2 and 3), but it should be mentioned that the pattern of daily activity could change within the season. Activity at night prevailed in the Betuleetum pilosae caricosum both in spring and in summer, but in the Piceetum coryloso-ruboso-oxalidosum nocturnal activity predominated in spring and diurnal activity in summer (Tab. 3). Such differences can be explained best with the characteristics of the behaviour of the most frequent species. In spring “nocturnal” species dominated in both types of forests. At the same time in summer *T. secalis*, the most frequent “diurnal” species, was active, and dominated in the Piceetum coryloso-ruboso-oxalidosum. Moreover, a second “diurnal” species, *L. pilicornis*, was captured in the same

biotope. Finally, seasonal changes in the characteristics of daily activity could be observed for some species. Among them, *P. melanarius* should be mentioned. In spring this species was active mainly at night, but in summer it was active mainly at day time. Changes of the pattern of daily activity within the season was also noted for some less frequent species (*Pterostichus aethiops* and *P. oblongopunctatus*).

The detailed study of daily activity in the periods of maximum activity revealed that in spring (Fig. 3a) most carabid species were active during the night hours. Two peaks can be observed: the first peak occurred between 23–24 p.m. (two hours after sunset) and the second one at 1–3 a.m. (two hours before sunrise). Such peaks were also mentioned by Thiele [1977].

During the period of maximum seasonal activity in the summer the course of the curve showing the activity at night does not differ much from the curve showing activity at day time, but the maximum of daily activity occurred at night hours (Fig. 3b). Such differences between the daily activity at spring and summer were connected with the ecological features of the dominant species. As it was already pointed out [Thiele, 1969] definite correlations of daily activity with the ecological preferences of the species exist. The analysis of the

Table 4. Daily activity of carabid beetles in Fraxinetum-Quercetum pilosae caricoso aegopodiosum (Voronezskaja region, forest-steppe).
Таблица 4. Суточная активность жужелиц в Fraxinetum-Quercetum pilosae caricoso aegopodiosum (Воронежская область, лесостепь).

Species	Day	Night	% of day activity	χ^2
<i>Calosoma inquisitor</i> L.	92	8	92.0	70.56
<i>Carabus stscheglovi</i> Mnh.	147	22	87.0	92.5
<i>C. cancellatus</i> Ill.	37	5	88.1	24.4
<i>Badister lacertosus</i> Sturm	22	11	66.7	3.67*
<i>Panagaeus bipustulatus</i> F.	20	3	87.0	12.6
<i>Pt. oblongopunctatus</i> F.	232	136	64.8	31.4
<i>Pt. melanarius</i> Ill.	204	68	75.0	68.0
<i>Harpalus latus</i> L.	47	9	83.9	25.8
Total	801	252	76.2	292.9

* — differences statistically not significant.

* — различия статистически недостоверны.

communities showed that almost all spring reproducing forest species were active at night because they are hibernophilic. Sometimes they show resistance against

cold temperatures as well. *Platynus assimilis* for example, the most abundant among the dominant species prefers temperatures between 6–10°C. On the contrary, species reproducing at summer/autumn are thermophilic. They prefer temperatures about 20°C. Due to the fact that in summer rather high temperatures may be registered even at night, diurnal (*T. secalis*) as well as nocturnal (*P. atrorufus*) activity predominates in species reproducing at summer/autumn.

In the forest-steppe in the Fraxinetum-Quercetum pilosae-caricoso-aegopodiosum the eight most abundant species all were mainly active at the light period of the day.

In the Quercetum convallarioso-rubosum diurnal activity was dominant, too. This is true both for the whole carabid beetle community and the most abundant species (*P. melanarius*, 52 specimens were caught) with 77.8% diurnal activity and 86.8% diurnal activity, respectively.

Discussion

The results of the study demonstrate that in carabid beetles, concerning the whole period of activity in the year, diurnal activity prevails in the forests of the middle taiga

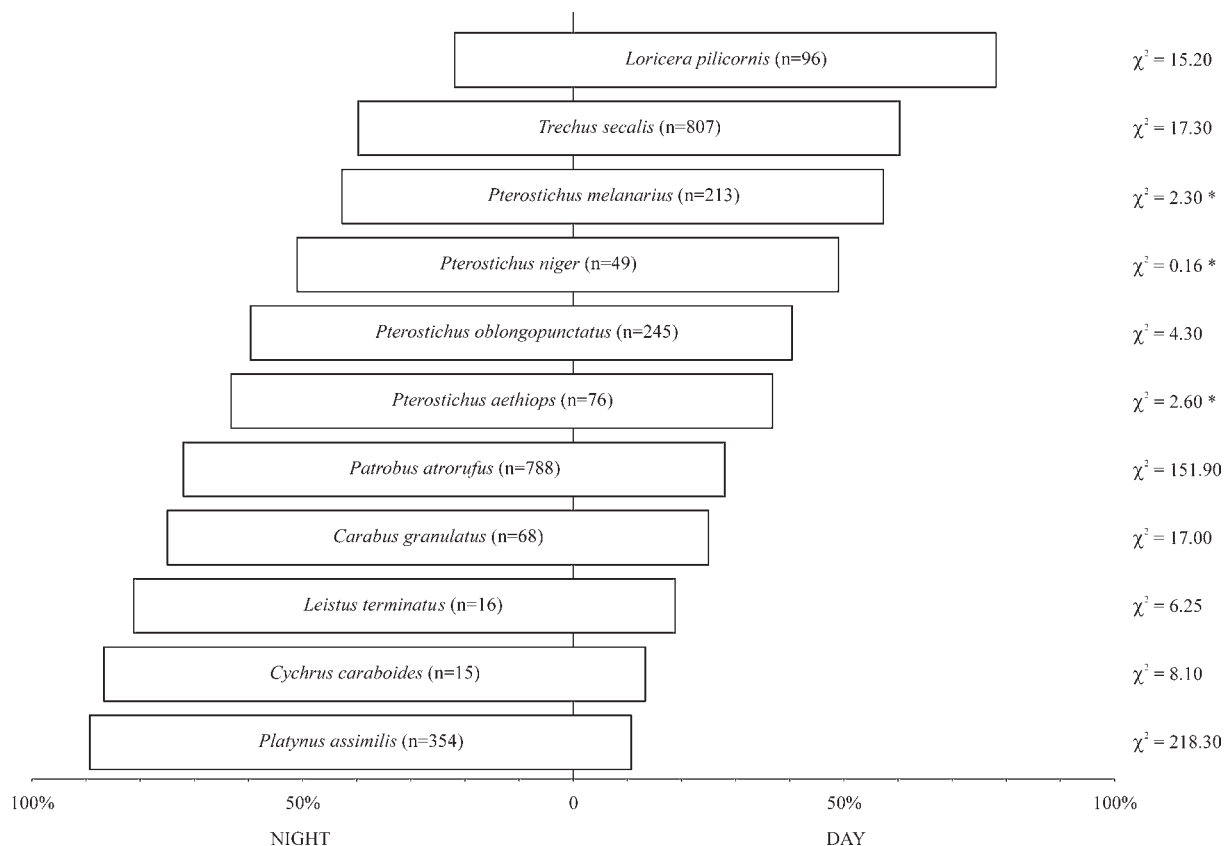


Fig. 2. The ratio between diurnal and nocturnal activity of some carabid species in the forests of broad-leaved spruce subzone.
* — differences statistically not significant.

Рис. 2. Соотношение дневной и ночной активности некоторых видов жужелиц подзоны широколиственных лесов. * — статистически недостоверные различия.

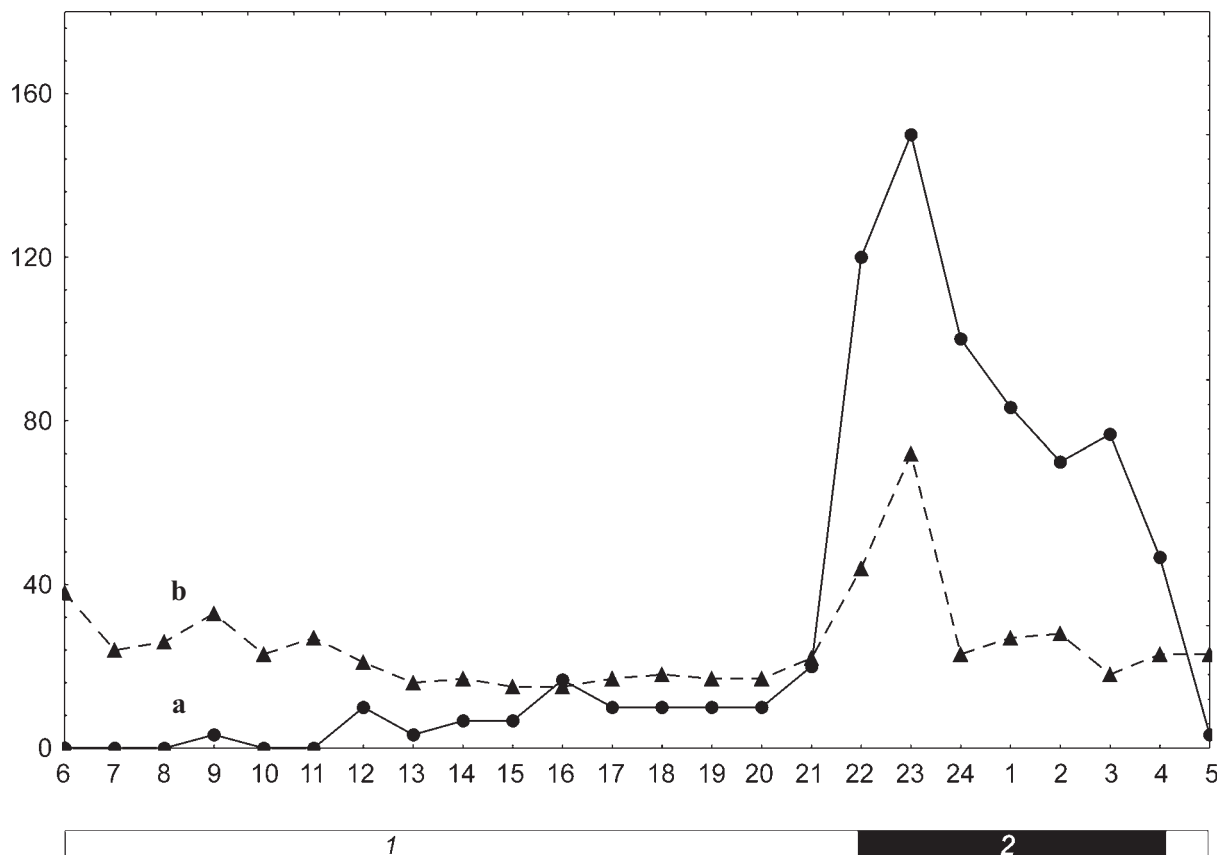


Fig. 3. Daily dynamics of activity of carabid beetles in (a) *Betuletum pilosae caricosum* and (b) in *Piceetum coryloso-ruboso-oxalidosum*. White rectangle day; black rectangle – night.

Рис. 3. Динамика суточной активности жуужелиц в (а) *Betuletum pilosae caricosum* и (б) в *Piceetum coryloso-ruboso-oxalidosum*. Белый прямоугольник – день; чёрный прямоугольник – ночь.

and the forest-steppe, whereas in the subzone of broad-leaved spruce forests nocturnal activity is dominant. Nocturnal activity is typical for carabids in the forests of Germany, too [Thiele, 1977; Stubbe et al., 1984].

There are several possibilities to explain differences concerning the daily activity within carabid beetle communities in different geographical zones. First, the differences may be explained by changes in species composition: in the middle taiga and forest-steppe mainly “diurnal” species predominate, whereas in the forests of broad-leaved spruce subzone “nocturnal” species are dominant. Secondly, the time of activity may change in one and the same species depending on the respective zone. Three species (*P. atrorufus*, *T. secalis* and *L. pilicornis*) out of the most abundant species dominated in two regions (Arkhangelskaja, and Moscow) and two species (*P. melanarius* and *P. oblongopunctatus*) dominated in all three regions. The data demonstrate (Tabs 1–4; Fig. 2) that in same species (*P. melanarius*, *T. secalis* and *L. pilicornis*) independently from the geographical zone the pattern of daily activity remains the same, whereas in other species (*P. atrorufus*, *P. oblongopunctatus*) changes occur.

The pattern of daily activity may also change in east-west direction. For example, *L. pilicornis* and the indif-

ferent species *Pterostichus niger* (Moscow region) belong in Germany to the group of “nocturnal species” [Thiele, 1977; Stubbe et al., 1984].

Moreover, in some species the preferred time of activity may change depending on the biotope. *L. pilicornis*, for example, is active in alder forests at daytime, but in willow stands mainly at night [Schiller & Weber, 1975].

Finally, seasonal changes in the activity pattern of some species may influence the overall picture of the community. This is clearly demonstrated by the species *P. atrorufus* and *C. micropterus* in the middle taiga and the species *P. melanarius* in the broad-leaved spruce subzone. The same changes in daily activity of *P. melanarius* in Belgium (fields near Gent) were already mentioned [Desender et al., 1985].

The above mentioned reasons (seasonal changes regarding time of activity, changes of the pattern of daily activity depending on the biotope and the season) may explain the seasonal changes of the pattern of daily activity in the *Piceetum coryloso-ruboso-oxalidosum* (broad-leaved spruce subzone).

According to the preferred time of daily activity in the forest in the studied regions four groups of species can be distinguished: exclusively diurnal, mainly diur-

nal, mainly nocturnal and indifferent. Moreover, the results demonstrate that from the north to the south a replacement of groups of species with different daily activity takes place. In the middle taiga exclusively "diurnal", mainly "diurnal" and indifferent species were recorded. In the broad-leaved spruce subzone we found mainly "nocturnal", mainly "diurnal" and indifferent species. In the forest-steppe zone mainly "diurnal" species were dominant and one indifferent species.

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