

Far Eastern Entomologist

Дальневосточный энтомолог

Journal published by Far East Branch
of the Russian Entomological Society
and Laboratory of Entomology, Federal
Scientific Center of the East Asia
Terrestrial Biodiversity, Vladivostok

Number 532: 1-16

ISSN 1026-051X (print edition)
ISSN 2713-2196 (online edition)

September 2025

<https://doi.org/10.25221/fee.532.1>

<https://elibrary.ru/amrtrm>

<https://zoobank.org/References/90C16727-F1D6-44E8-BD81-407CEF3B2C49>

ASSEMBLAGES OF DUNG BEETLES (COLEOPTERA, SCARABAEOIDEA) LIVING IN THE DUNG OF WILD ANIMALS IN THE RUSSIAN FAR EAST. COMMUNICATION 1. INHABITANTS OF THE DUNG OF THE SIKA DEER (*CERVUS NIPPON*)

S. A. Shabalin

*Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far East
Branch of the Russian Academy of Sciences, Vladivostok, 690022, Russia. E-mail:
oxecetonia@mail.ru*

Summary. In the south of the Russian Far East an assembly of dung beetles inhabiting sika deer dung has been studied. Data on the species composition, population dynamics, and number and biomass of the dung beetles are presented. Comparisons of assemblies of dung beetles that inhabit wild and domestic mammals show that the species composition of these assemblies as well as the dynamic processes taking place in them have significant differences. This is expressed in a richer species composition and number of species in individual functional groups in cow dung, and poor species composition in sika deer dung, in differences in dominant species, features of the seasonal distribution of abundance and biomass (including peak values of these indicators for individual functional groups of dung beetles), and aggregate indicators of overlap of temporal aspects ecological niches of coprophilous Coleoptera.

Key words: coprophilous, scarabaeoid beetles, assembly, seasonal dynamic, niches interception, biodiversity, Primorskii krai, Russia.

С. А. Шабалин. Сообщества навозников (Coleoptera, Scarabaeoidea), обитающих в помёте диких животных Дальнего Востока России. Сообщение 1. Обитатели помёта пятнистого оленя (*Cervus nippon*) // Дальневосточный энтомолог. 2025. N 532. С. 1-16.

Резюме. На юге Дальнего Востока России изучена ассамблея навозников, обитающих в помёте пятнистого оленя. Приведены данные о видовом составе, динамике населения, численности и биомассе навозников. Сравнение ассамблей навозников, обитающих в помёте диких и домашних млекопитающих, показывает, что их видовой состав и протекающие в них динамические процессы имеют существенные различия. Это выражается в более богатом видовом составе и числе видов отдельных функциональных групп в коровьем помёте и бедном видовом составе в помёте пятнистого оленя, в различиях в составе доминирующих видов, особенностях сезонного распределения численности и биомассы (включая пиковые значения этих показателей для отдельных функциональных групп навозников), а также в совокупных показателях перекрытия временных аспектов экологических ниш копрофильных жесткокрылых.

INTRODUCTION

Due to their distribution around the world and taxonomic and ecological diversity, coprophilous scarabaeoid beetles (Coleoptera: Scarabaeoidea) are a good model object for studying the structure, dynamics, and features of the organization and functioning of insect assemblies (Spector, 2006; Nichols *et al.*, 2008; Ortega-Martínez *et al.*, 2020). Many publications are devoted to the study of assemblies of dung beetles from various regions and countries (Hanski, Cambifort, 1991; Simmons & Ridsdill-Smith, 2011; Scholtz, *et al.*, 2012; *etc.*). Being an ephemeral trophic resource, the excrement of certain species of vertebrates has varying accessibility to dung beetles. The availability of excrement to coprophagous insects varies greatly in time and space and can be essential for the stabilization or fluctuation of populations of these insects. Trophic selection can play an important role in the coexistence of species and subsequent sharing of resources (Martín-Piera & Lobo 1996; Filgueiras *et al.*, 2009; Tocco *et al.*, 2018).

In Russia, the study of dung beetle assemblies is at the initial stages. A.M. Psarev examined the participation of dung beetles in the structure of coprobiont insect communities using pastures in the south of Western Siberia (Psarev, 2016). In the Russian Far East, we have considered only some assemblies of these beetles in sheep, cow and horse droppings (Shabalin, 2020, 2021, 2022a, 2024); inhabitants of sika deer dung have not previously been studied in this respect. Accordingly, it is of interest to study the assemblage of dung beetles that inhabit sika deer dung and compare it with that in dung of domestic mammals, which will allow us to assess the role of trophic selection and the influence of the local pool of species on the structure of assemblies. The purpose of this work is to study dung beetles that inhabit sika deer dung in the Safari-park (south of Primorskiy krai, Shkotovskiy district) and

compare the results with data previously obtained on the dung of domestic mammals (Shabalin, 2020, 2021, 2022a, 2024) to identify the features of the morphology and dynamics of the assemblies coprophages, determined by the type of droppings of mammals in Primorskii krai. With this article we begin a series of publications devoted to the study of assemblages of dung beetles, inhabitants of the dung of wild mammals in the Russian Far East.

MATERIAL AND METHODS

The collection of beetles, both in sika deer droppings, was carried out in the south of Primorskii krai (Shkotovskii district) in the vicinity of Shkotovo (43°32' N, 132°40' E) on the Safari-park in enclosures using substrate removal (Shabalin, 2021) from April 3 to October 26, 2020, once every ten days. The species identification of Coleoptera was carried out using the Key to Insects of the Far East (Berlov, 1989), review works (Kabakov, 2006), and considering new faunal finds (Shabalin & Berlov, 2008; Shabalin, 2018; Shabalin *et al.*, 2024). The collection of the Federal Scientific Center for Biodiversity, Far Eastern Branch, Russian Academy of Sciences, was used as comparative material. Over the entire period of the study, 106 L of dung were removed and distilled and more than 751 individuals of coprophilous scarabaeoid coleoptera were collected and identified. Taxon names are given according to the Catalog of Palaearctic Coleoptera (Dellacasa *et al.*, 2016; Nikolajev *et al.*, 2016; Ziani & Bezděk, 2016).

Functional groups are distinguished by a combination of trophodynamic relationships of beetles and their size classes. Types of trophodynamic relationships are given according to I. Hanski & Y. Cambifort (1991): dwellers are beetles that live in the thickness of manure; tunnelers are beetles that make passages under a pile of substrate and store provisions for larvae, and rollers are beetles that roll balls of dung.

The following size classes of beetles are accepted: small (s), up to 4.7 mm; medium (m), from 4.7 to 8.0 mm; and large (l), more than 8 mm (Shabalin, 2023). To calculate biomass indicators, original data were used (Shabalin, 2023), considering the regional specifics of the fauna. The overlap of ecological niches of beetles was assessed using formulas (Colwell & Futuyama, 1971; Hanski, 1978; Yu & Orloci, 1990):

$$PS_{ik} = 1 - \frac{\sum_j |p_{ij} - p_{kj}|}{2} \quad (1), \text{ and}$$

$$PS_{ik} = \sum_j \min(p_{ij}, p_{ik}) \quad (2),$$

where PS_{ik} is the overlap of ecological niches for species i and k , p_{ij} is the share of species i at point in time j , and p_{kj} is the share of species k at point in time j . In formula (1), the complete overlap of ecological niches takes values equal to 0; the absence of overlap equals 1. In formula (2), complete overlap takes a value equal to 1, and the absence of overlap takes a value equal to 0. Threshold values are defined for the first formula as less than 0.8 and, for the second, more than 0.1. Calculations

were performed in EstimateSWin910, Past 3.26, and Excel 2007 programs. When analyzing the seasonal aspects of a beetle population, species diversity refers to the number of species active at the adult stage of development.

RESULTS

Species composition, functional groups. A total of 751 individuals of beetles belonging to 14 species were collected and identified, the list of which is given below.

Family Geotrupidae: *Geotrupes* (*Geotrupes*) *koltzei* Reitter, 1892, *Phelotrupes* (*Chromogeotrupes*) *auratus* (Motschulsky, 1858).

Family Scarabaeidae, subfamily Scarabaeinae: *Caccobius* (*Caccobius*) *brevis* Waterhouse, 1875, *Caccobius* (*Caccophilus*) *christophi* Harold, 1879, *Caccobius* (*Caccophilus*) *sordidus* Harold, 1886, *Onthophagus* (*Altonthophagus*) *uniformis* Heyden, 1886, *Onthophagus* (*Gibbonthophagus*) *atripennis* Waterhouse, 1875, *Onthophagus* (*Onthophagus*) *bivertex* Heyden, 1887.

Family Scarabaeidae, subfamily Aphodiinae: *Acrossus superatratus* (Nomura et Nakane, 1951), *Agrilinus ater* (DeGeer, 1774), *Aphodaulacus koltzei* (Reitter, 1892), *Esymus pusillus* (Herbst, 1789), *Labarrus sublimbatus* (Motschulsky, 1860), *Phaeaphodius rectus* (Motschulsky, 1866).

The expected species diversity in the studied assembly of Coleoptera was assessed using the Chao2 and Mao Tao functions (Fig. 1); the values obtained at the terminal points of the functions were 14.31 and 14.94 species; and the identified diversity was 94.83 and 93.77% of that theoretically expected, respectively. The share of identified species in the assembly of dung beetles inhabiting sika deer dung in the Safari-park is 18.67% of the fauna of these beetles in the south of Sikhote-Alin Mountains (Shabalin, 2022b).

Coleoptera are classified into four functional groups based on trophodynamic relationships and size classes. The most well represented groups are tunnelers the large (4 species) as well a medium size class (4 species); in the groups of dwellers only 3 species were recorded in each, the groups of small and medium size class dwellers.

Seasonal aspects of changes in species composition. The activity of imago beetles is observed from the beginning of April and continues until the second ten days of October. In the first and second ten days of April, only small-sized *Aphodaulacus koltzei* dweller is found in the collections. In the third ten days of April, medium-sized dweller *Phaeaphodius rectus* is added to it. In the first ten days of May medium-sized tunnelers appear (*Caccobius christophi*). From the first ten days of April to the first ten days of June, the number of species increases, from 1 to 7 species. From the second ten days of June to the end of June a decrease in species diversity occurs. Thus, in this period only dwellers were activity. The maximum taxonomic diversity of beetles inhabiting sika deer dung in the Sikhote-Alin Mountains is noted in the first-second ten days of July (9 species). In the third ten day of July was only large-size tunnelers *Phelotrupes auratus*. From the first ten days of August to third ten days of September, taxonomic diversity consists of species with

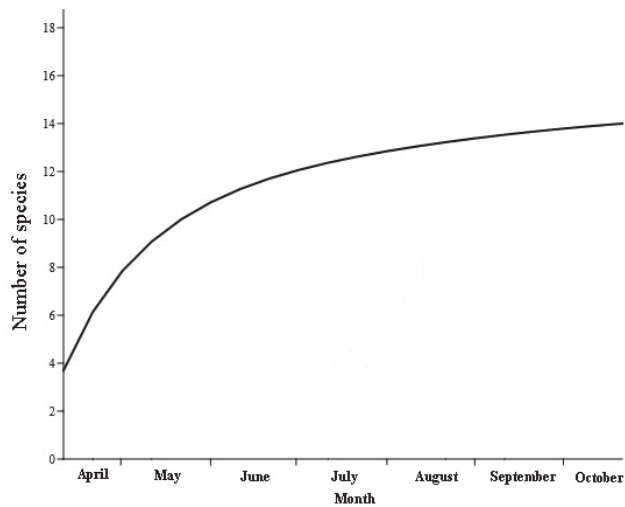


Fig. 1. Accumulation curve (Mao Tao) of dung beetle species.

an extended period of adult activity (*Geotrupes koltzei*, *Phelotrupes auratus*, *Caccobius christophi*, and *Phaeaphodius rectus*). From the first ten days of October to the second ten days of October, diversity decreases sharply. In the third ten days of October, with a strong decrease in daytime temperatures, beetle activity stops (Fig. 2).

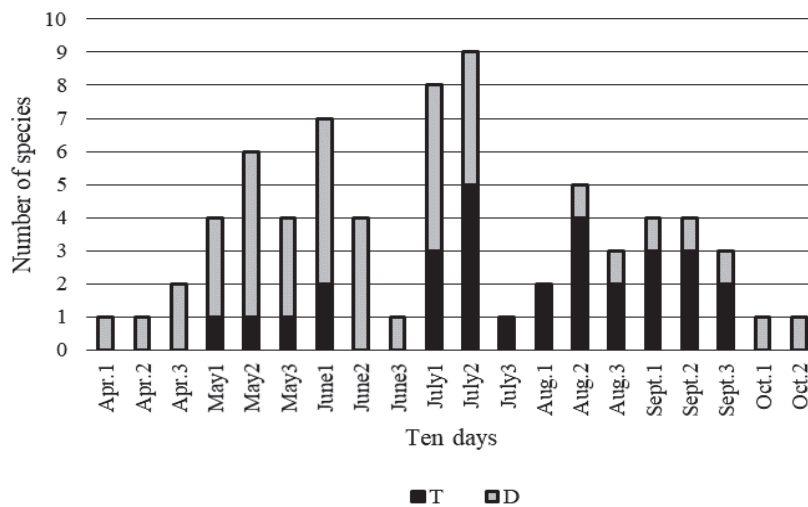


Fig. 2. Seasonal dynamics of the number of species. Trophodynamic groups: T – beetles making passages under a pile of substrate and storing provisions for the larvae, D – beetles living in the depth of manure.

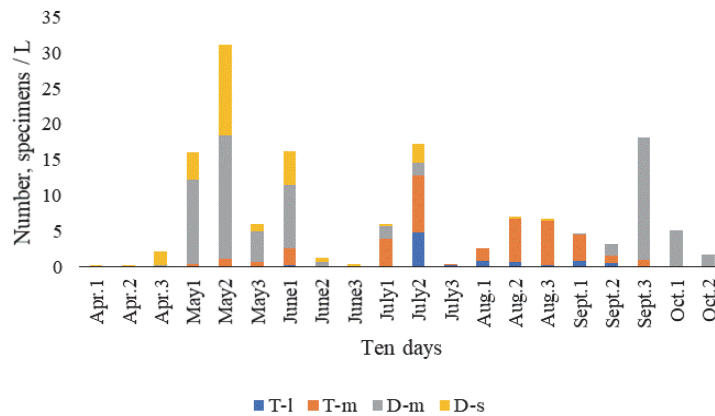


Fig. 3. Seasonal population dynamics. Trophodynamic groups: T – beetles making passages under a pile of substrate and storing provisions for the larvae; D – beetles living in the depth of manure. Size classes: l – large; m – medium; s – small.

Number and seasonal aspects of its changes. In the conditions of the Safari-Park, during the growing season, one peak of increase in the number of coprophilous scarabaeoid Coleoptera are observed in sika deer dung, with their number exceeding 30 individuals/ L. This peak with a total number of dung beetles of 31.11 individuals/L, falls on the second ten days of May. This peak is formed primarily due to the high performance of the small dwellers *Aphodaulacus koltzei* (7.56 individuals/L) and *Esymus pusillus* (5.11 individuals/L), and midsize dweller *Agrilinus ater* (9.33 individuals/L). In general, the growing season is characterized by very low numbers of beetles.

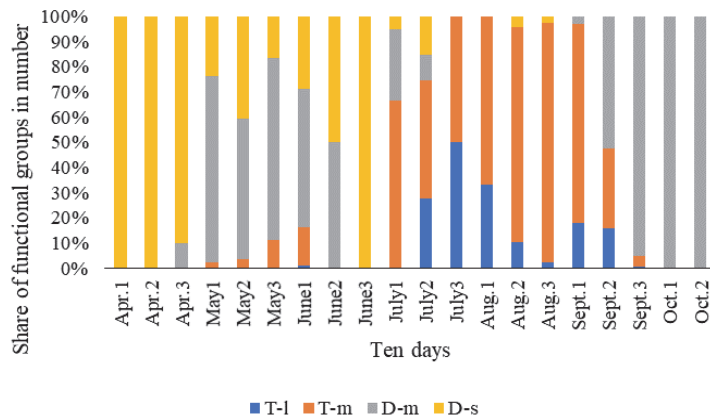


Fig. 4. Proportion of functional groups in the number of beetles. Designations of months and functional groups of beetles are the same as in fig. 3.

Table 1. Number of dung beetles (specimens/L) in t sika deer dung by ten-day periods (first ten days of April – first ten days of July)

Species	Decades									
	Apr.1	Apr.2	Apr.3	May1	May2	May3	June1	June2	June3	July1
<i>Ph. auratus</i>	–	–	–	–	–	–	0,17	–	–	–
<i>C. christophi</i>	–	–	–	0,40	1,11	0,67	2,33	–	–	4,00
<i>C. sordidus</i>	–	–	–	–	–	–	–	–	–	0,15
<i>C. brevis</i>	–	–	–	–	–	–	–	–	–	0,15
<i>A. superatratus</i>	–	–	–	0,60	2,89	–	1,33	–	–	0,46
<i>A. ater</i>	–	–	–	11,20	9,33	4,00	4,67	0,17	–	0,15
<i>A. koltzei</i>	0,20	0,25	2,00	3,80	7,56	–	0,17	–	–	–
<i>E. pusillus</i>	–	–	–	–	5,11	1,00	4,50	0,17	0,33	0,15
<i>L. sublimbatus</i>	–	–	–	–	–	–	–	0,50	–	0,15
<i>Ph. rectus</i>	–	–	0,22	–	5,11	0,33	2,83	0,50	–	1,08

Table 2. Number of dung beetles (specimens/L) in t sika deer dung by ten-day periods (the second ten days of July – the second ten days of October)

Species	Decades									
	July2	July3	Aug.1	Aug.2	Aug.3	Sept.1	Sept.2	Sept.3	Oct.1	Oct.2
<i>G. koltzei</i>	–	–	–	0,14	–	–	0,17	–	–	–
<i>Ph. auratus</i>	4,40	0,20	0,89	0,29	–	0,43	–	–	–	–
<i>C. christophi</i>	3,20	–	0,89	5,71	6,17	3,00	1,00	0,77	–	–
<i>C. brevis</i>	0,20	–	–	–	–	–	–	–	–	–
<i>O. uniformis</i>	0,20	–	–	0,29	0,17	0,43	0,33	0,15	–	–
<i>O. atripennis</i>	0,20	–	–	–	–	–	–	–	–	–
<i>O. bivertex</i>	0,20	–	–	–	0,17	0,29	–	–	–	–
<i>A. superatratus</i>	0,20	–	–	–	–	–	–	–	–	–
<i>E. pusillus</i>	0,80	–	–	–	–	–	–	–	–	–
<i>L. sublimbatus</i>	1,80	–	–	0,29	0,17	–	–	–	–	–
<i>Ph. rectus</i>	1,60	–	–	–	–	0,14	1,67	17,23	5,11	1,71

The number of tunnelers during the growing season has two peaks. The first significant peak occurs in the second ten days of July, there is a small second peak in second – three ten days of August. It should be noted that, among tunnelers, the second peak accounts for 33.27% of the total annual number of these beetles. The seasonal dynamics of the number of tunnelers of the middle size class is similarly expressed; the peaks of their numbers correspond to the peaks of the number of tunnelers as a whole, and August accounts for 33.81% of the total annual number of this functional group of dung beetles. All these peaks are due to the high abundance of the medium-sized tunnelers *Caccobius christophi* (5.71 – 6.17 individuals/L). Large tunnelers are generally not numerous; only from the second ten days of July does the number of beetles of this group reach values above 4.8 individuals/L, and

this period accounts for 56.80% of the total annual number of beetles of this group, while during the rest of the period, the abundance indicators do not exceed 0.88 individuals/L (Figs 3, 4). This peak is formed primarily due to the high performance of the large tunnelers *Phelotrupes auratus* (4.40 individuals/L).

High numbers (more than 15 individuals/L) of dwellers were noted from the first ten days of May to the second ten days of May, as well as in the third ten days of September, which is 44.93, and 16.98% of their annual numbers, respectively (Table 1, 2). From the third ten days of July to the first ten days of August, no dwellers were observed. A significant share of the annual number of dwellers falls on the periods from the third ten days of May to the first ten days June, from the first ten days of July to the first ten days of August, and from the third ten days of September to the first ten days of October (Figs 3, 4). For the functional group of dwellers of the medium size class, population peaks were noted from the first – second ten days of May and the third ten days of September. The spring peak in the number of medium sized dwellers is due to high rates of *Agrilinus ater*, and the autumn peak due to the same species and *Phaeaphodius rectus*. Small dwellers had population peaks second ten days of May, mainly due to high numbers of *Aphodaulacus koltzei* and *Esymus pusillus* (Table 1, 2).

Biomass and seasonal aspects of its changes. In the collection of beetles under consideration, one peak in the rise in biomass values were noted in the second ten days of July. This peak consists of high values for large tunnelers (Fig. 5, 6).

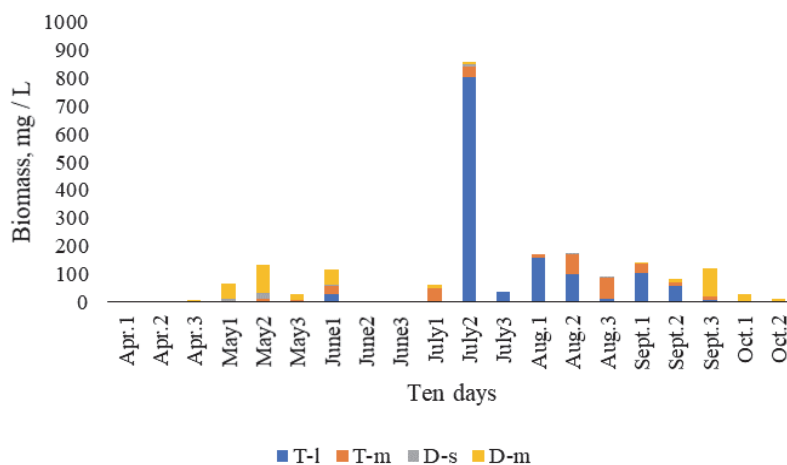


Fig. 5. Seasonal dynamics of biomass. Designations of months and functional groups of beetles are the same as in fig. 3.

The peak rise in the biomass of large tunnels was noted in the second ten days of July; this period accounts for 61.31% of their annual biomass, mainly due to high values of *Phelotrupes auratus*. Medium-sized tunnels have a peaks biomass in the

first – second ten days of July, and second – third ten days of August, these periods account for 25.34% and 40.23% of their annual biomass. These peaks are due to high biomass values of *Caccobius christophi* (Table 3, 4).

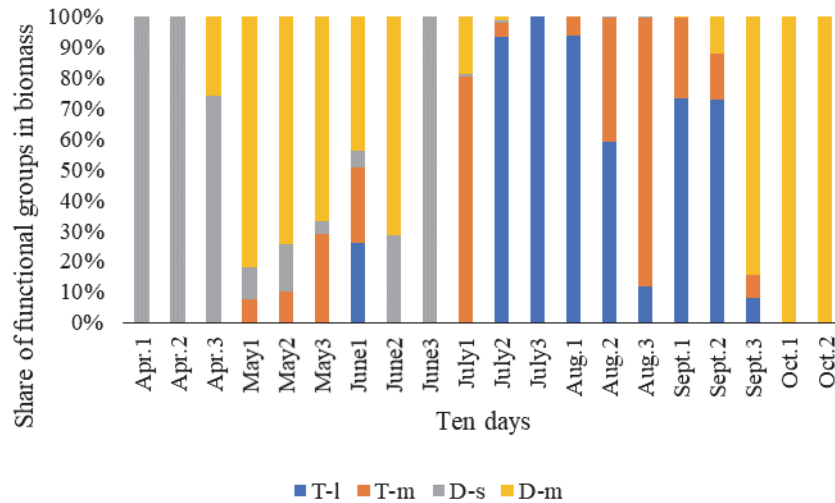


Fig. 6. Proportion of functional groups in biomass. Designations of months and functional groups of beetles are the same as in fig. 3.

Table 3. Dynamics of specific biomass of dung beetles (mg/L) in the sika deer dung by ten-day periods (first ten days of April – first ten days of July)

Species	Decades									
	Apr.1	Apr.2	Apr.3	May1	May2	May3	June1	June2	June3	July1
<i>G. koltzei</i>	–	–	–	–	–	–	–	–	–	–
<i>Ph. auratus</i>	–	–	–	–	–	–	29,70	–	–	–
<i>C. christophi</i>	–	–	–	4,88	13,56	8,13	28,47	–	–	48,80
<i>C. sordidus</i>	–	–	–	–	–	–	–	–	–	1,40
<i>C. brevis</i>	–	–	–	–	–	–	–	–	–	0,89
<i>A. superatratus</i>	–	–	–	6,41	30,85	–	14,24	–	–	4,93
<i>A. ater</i>	–	–	–	47,38	39,48	16,92	19,74	0,71	–	0,65
<i>A. koltzei</i>	0,37	0,46	3,70	7,03	13,98	–	0,31	–	–	–
<i>E. pusillus</i>	–	–	–	–	6,54	1,28	5,76	0,21	0,43	0,20
<i>L. sublimbatus</i>	–	–	–	–	–	–	–	1,22	–	0,38
<i>Ph. rectus</i>	0,00	0,00	1,29	0,00	29,75	1,94	16,49	2,91	–	6,27

Table 4. Dynamics of specific biomass of dung beetles (mg/L) in sika deer dung by ten-day periods (the second ten days of July – the second ten days of October)

Species	Decades									
	July2	July3	Aug.1	Aug.2	Aug.3	Sept.1	Sept.2	Sept.3	Oct.1	Oct.2
<i>G. koltzei</i>	–	–	–	33,47	–	–	39,05	–	–	–
<i>Ph. auratus</i>	784,04	35,64	158,39	50,91	–	76,37	–	–	–	–
<i>C. christophi</i>	39,04	–	10,84	69,71	75,23	36,60	12,20	9,38	–	–
<i>C. brevis</i>	1,16	–	–	–	–	–	–	–	–	–
<i>O. uniformis</i>	12,09	–	–	17,27	10,08	25,91	20,15	9,30	–	–
<i>O. atripennis</i>	6,14	–	–	–	–	–	–	–	–	–
<i>O. bivertex</i>	3,80	–	–	–	3,17	5,43	–	–	–	–
<i>A. superatratus</i>	2,14	–	–	–	–	–	–	–	–	–
<i>E. pusillus</i>	1,02	–	–	–	–	–	–	–	–	–
<i>L. sublimbatus</i>	4,39	–	–	0,70	0,41	–	–	–	–	–
<i>Ph. rectus</i>	9,31	–	–	–	–	0,83	9,70	100,28	29,75	9,98

For small dwellers, increases in biomass indicators have been established from the second ten days of May. This, most significant, peak accounts for 42.41% of the annual biomass of this group, primarily due to the high abundance of *Aphodaulacus koltzei*. Increases in the biomass of medium-sized dwellers were noted in the second ten days of May in the third ten days of September. The spring (second ten days of May) period accounts for 24.90% and the autumn period 24.95% of the annual biomass of beetles of this group. Similar to the peaks in the number of medium-sized dwellers, the summer peak of biomass in this group is associated with high rates of *Acrossus superatratus* and *Agrilinus ater*, but the autumn with *Phaeaphodius rectus* (Table 3, 4).

Distribution of species by abundance. The distribution of species in the space log of the number of specimens – the rank of species graphically looks like a straight line (Fig. 7). The resulting linear model with a sufficiently high coefficient of determination corresponds to a geometric series or niche interception hypothesis. It is known that such a geometric model is closest to the series of significance of species for individual assemblies that are part of communities, when the dominance of a small number of species is clearly expressed (Giller, 1988), and a significant part of the species is represented by only a small number of individuals. In addition, a geometric series can express the outcome of competition for niche capture between a limited number of species (Whittaker, 1980), depending on the same environmental resources.

Overlapping ecological niches. The overlap of temporal aspects of ecological niches for tunnelers in sika deer dung in general, considering threshold values, was established for 14 pairs of species (out of the maximum possible combination, 28 pairs), of which 7 pairs of species belong to the same size groups (25.00% of the

maximum possible combination): *Ph. auratus* – *O. uniformis*, *C. christophi* – *C. sordidus*, *C. christophi* – *C. brevis*, *C. christophi* – *O. bivertex*, *C. sordidus* – *C. brevis*, *C. brevis* – *O. bivertex*, and *O. uniformis* – *O. atripennis*.

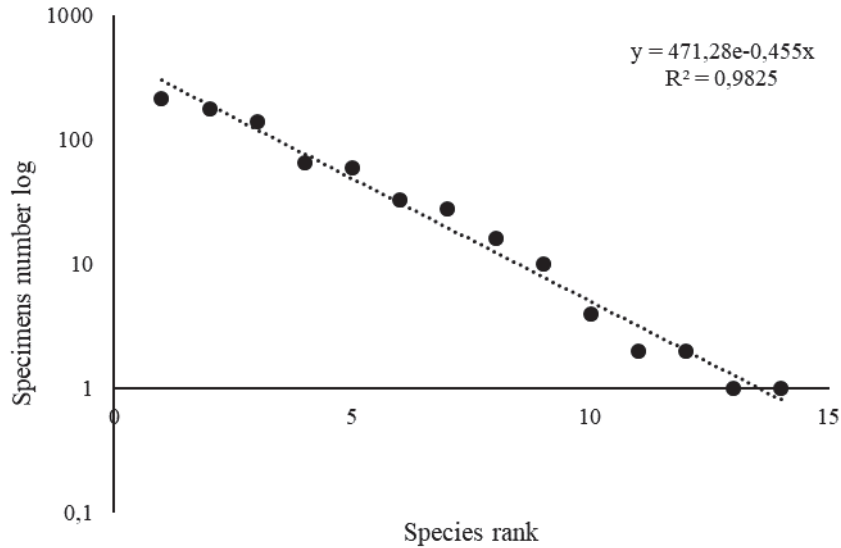


Fig. 7. Rank distribution of species.

For dwellers, such an overlap of temporal aspects of ecological niches were obtained for 8 pairs of species out of the maximum possible combination of 20 pairs. Generations *Phaeaphodius rectus* divided into spring (s) and autumn (a). Considering the differentiation of beetles by size classes, 4 pairs of species are presented (20.00% of the maximum possible combination), for which there is a significant overlap of temporal aspects of ecological niches: *A. superatratus* – *A. ater*, *A. superatratus* – *Ph. rectus* (s), *A. ater* – *Ph. rectus* (s), and *A. koltzei* – *E. pusillus*.

DISCUSSION

The results obtained are the first in the Russian Far East to study the assemblages of dung beetles inhabiting in the dung of wild animals. Although the data are preliminary, they allow comparison with previously obtained data on the dung beetles population of some domestic animals. Previously, we examined the assemblages of dung beetles in the south of Russian Far east inhabiting in the droppings of sheep (Shabalin, 2020, 2021), cow (Shabalin, 2024) and horse (Shabalin, 2022a).

The assemblage of inhabitants of sika deer dung is less taxonomically diverse, with 14 species recorded, while in sheep dung there are 29 species, in cow dung there are 36 species, and in horse dung are 20 species. In the assemblages under consideration, beetles belong to two families. The sika deer droppings also show a low number of functional groups of beetles. Only 4, while the droppings of domestic animals contain 5-6 such groups. A previously conducted analysis of the food specialization of dung beetles in the Russian Far East showed that the droppings of wild animals are significantly poorer in species than the droppings of farm animals. In addition, the species composition of beetles noted in the droppings of sheep and deer occupies an intermediate position. On the one hand, it is richer and more original than the droppings of predatory animals and wild boars, and on the other hand, it is significantly poorer and more banal than cows and horses (Shabalin, 2025).

The period during which the beetles were noted in the sika deer droppings coincides with the period for beetles noted in the droppings of horses and sheep in Sikhote-Alin Mountains (Shabalin, 2020, 2022a). But this is shorter than for beetles noted in the droppings of cows and sheep in the northern spurs of the Manchurian-Korean Mountains (Shabalin, 2021, 2024). These features are probably due to weather and climate conditions. The maximum taxonomic diversity of beetles inhabiting sika deer dung is a typical for the Sikhote-Alin Mountains. This period falls at the beginning to the middle of summer.

Peaks in the number of beetles in the sika deer dung, as a sheep dung in Sikhote-Alin Mountains consideration occur mainly during similar periods with minor fluctuations. So, if in sheep droppings and the sika deer dung the spring peak falls on the second ten days of May, but the autumn peak in sika deer droppings was not noted. In addition, these peaks, although formed mainly due to the high number of dwellers, are due to increases in the numbers of predominantly different species. Peaks in the number of beetles in the sika deer dung, horse dung and cow dung occur at different periods. In general, the peaks in the numbers of dung beetles inhabiting in the droppings of sika deer, cows, horses and sheep occur at different times. However, for groups of medium sized and small dwellers, these periods coincide with small fluctuations and occur in spring and autumn. In addition, these peaks, although formed mainly due to the high number of dwellers, are due to increases in the numbers of predominantly different species.

The biomass of dung beetles living in both sika deer and some domestic animals is characterized by peak values at approximately the in different time. The peak biomass levels of large tunnellers have a significant impact on these differences. However, the role of individual functional groups in the formation of biomass is the same. The peaks of biomass medium and small dwellers and medium tunnelers in sika deer dung and some domestic animals in Primorskii krai occur in approximately equal periods with small fluctuations, probably due to local geographical and weather factors.

The rank distribution of species in the considered assemblages corresponds to a geometric series or niche interception hypothesis. However, lower exponents were

obtained for cow dung, which corresponds to a sharper slope of the function line and a more pronounced dominance of a small number of taxa. Considering the overlap of temporal aspects of the ecological niches of dung beetles in sika deer droppings, it should be noted that the aggregate indicators of this parameter for tunnelers dwellers are comparable, but for dwellers they differ significantly. For the inhabitants, the overlap of the temporal aspects of ecological niches was found in the dung of the sika deer to be 2-3 times greater than the maximum possible combination of pairs of species than in cow or sheep.

The above comparisons of dung beetle assemblies inhabiting in dung of domestic and sika deer dung show that, although these assemblies are located in the same place, they were formed on the basis of a common pool of species and have a similar species composition of beetles, but the structural features of these assemblies, as well as those dynamic processes occurring in them, have significant differences. This is expressed in a poorer species composition and number of species in individual functional groups in sika deer droppings, differences in dominant species, features of the seasonal distribution of abundance and biomass (including peak values of these indicators for individual functional groups of dung beetles), and aggregate indicators of the overlap of temporal aspects of ecological niches of coprophilous scarabaeoid Coleoptera. Apparently, these differences are due to a number of factors, among which we should note the historical processes of the formation of assemblies of coprophilous scarabaeoid Coleoptera in the region under consideration.

Large cow or horse excrement dehydrates over a long period of time, retaining its attractiveness to beetles for longer. This becomes most relevant with the establishment of high positive temperatures. Sheep droppings or sika deer droppings are small in size and dehydrate faster than cow droppings, but are able to rehydrate and become attractive to beetles again. Since a dense crust forms on the surface of cattle manure when it is on the soil, which prevents the evaporation of moisture from the thickness of the manure, it is accessible to beetles for a long time. In addition, the large size of cow dung, when compared to sheep dung, makes it possible to maintain smoothed hydrothermal conditions for a longer time, and it remains attractive to coprophilous beetles for a long time. The settling of sheep or sika deer droppings in summer, a period with high daytime temperatures, is possible only for a short time.

CONCLUSIONS

Comparisons of assemblies of dung beetles that inhabit wild and domestic mammals show that the species composition of these assemblies, and the dynamic processes taking place in them have significant differences. This is expressed in a richer species composition and number of species in individual functional groups in cow dung, in differences in dominant species, features of the seasonal distribution of abundance and biomass (including peak values of these indicators for individual functional groups of dung beetles), and aggregate indicators of overlap of temporal aspects ecological niches of coprophilous Coleoptera.

The above differences are probably associated with the historical processes of the formation of assemblies of coprophilous scarabaeoid Coleoptera in the region under consideration and the size and structure of excrement of vertebrate animals. Cattle excrement is rich in moisture, dehydrates over a long period of time, and more smoothed hydrothermal conditions are formed in them, which makes it possible for this substrate to maintain a long-term attractiveness for coprophilous Coleoptera.

The further study of assemblies of dung beetles of large mammals in the south of Primorskii krai will make it possible to substantiate the hypothesis about the formation of the modern fauna of this group of Coleoptera in the study region, determine the mechanisms of formation of assemblies, and establish the leading factors limiting the diversity of beetles in these assemblies.

ACKNOWLEDGEMENTS

The research was carried out within the state assignment of Ministry of Science and Higher Education of the Russian Federation (theme No. 124012400285-7).

REFERENCES

- Berlov, E.Ya. 1989. 6. Subfamily Aphodiinae. P. 387–402. In: Lehr, P.A. (Ed.). *Key to the insects of Soviet Far East. Vol. III. Coleoptera. Pt. I.* Nauka, Leningrad. [In Russian]
- Colwell, R.K. & Futuyma, D.J. 1971. On the measurement of niche breadth and overlap. *Ecology*, 52(4): 567–576.
- Dellacasa, M., Dellacasa, G., Král, D. & Bezděk, A. 2016. Tribe Aphodiini Leach, 1815. P. 98–155. In: Löbl, I., Löbl, D. (Ed.). *Catalogue of Palaearctic Coleoptera. Vol. 3. Scarabaeoidea – Scirtoidea – Dascilloidea – Buprestoidea – Byrrhoidea. Revised and Updated Edition.* Brill, Leiden, Boston.
- Filgueiras, B.K.C., Liberal, C.N., Aguiar, C.D.M., Hernández, M.I.M. & Ianuzzi, L. 2009. Attractivity of omnivore, carnivore and herbivore mammalian dung to Scarabaeinae (Coleoptera, Scarabaeidae) in a Tropical Atlantic Rainforest remnant. *Revista Brasileira de Entomologia*, 53(3): 422–427.
- Hanski, I., Cambefort, Y. (Ed.). 1991. *Dung beetle ecology.* Princeton, New Jersey: Princeton University Press. 481 p.
- Hanski, I. 1978. Some comments on the measurement of niche metrics. *Ecology*, 59(1): 168–174.
- Kabakov, O.N. 2006. *The Lamellicorn Beetles of the Subfamily Scarabaeinae (Coleoptera: Scarabaeidae) of the Fauna of Russia and Adjacent Countries.* KMK, Moscow. 374 p. [In Russian]
- Martin-Piera, F. & Lobo, J.M. 1996. A comparative discussion of trophic preferences in dung beetles communities. *Miscellanea Zoológica*, 19(1): 13–31.
- Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezcua, S., & Favila, M.E. 2008. Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biological Conservation*, 141(6): 1461–1474. DOI: 10.1016/j.biocon.2008.04.011

- Nikolaev, G.V., Kral, D., & Bezděk, A. 2016. Family Geotrupidae Latreille, 1802. P. 33–52. In: Löbl, I., Löbl, D. (Ed.). *Catalogue of Palaearctic Coleoptera. Vol. 3. Scarabaeoidea – Scirtoidea – Dascilloidea – Buprestoidea – Byrrhoidea. Revised and Updated Edition.* Brill, Leiden, Boston.
- Ortega-Martinez, I.J., Moreno, C.E., Rios-Diaz, C.L., Arellano, L., Rosas, F. & Castellanos, I. 2020. Assembly mechanisms of dung beetles in temperate forests and grazing pastures, *Scientific Reports*, 10: 391. DOI: 10.1038/s41598-019-57278-x
- Psarev, A.M. 2016. *Fauna and Ecology of Beetles of Pastures in the Russian Altai.* Altai Gos. Gumanitarno-Pedagog. University. im.V.M. Shukshina, Biysk. 185 p. [In Russian]
- Scholtz, C., Davis, A. & Kryger, U. 2012. *Evolutionary Biology and Conservation of Dung Beetles.* Pensoft Publishers. 566 p.
- Shabalin, S.A. 2018. First record of *Sinodiapterna songrini* (Stebnicka et Galante, 1992) (Coleoptera: Scarabaeidae) from Russia. *Far Eastern Entomologist*, 363: 8–10. DOI: 10.25221/fee.363.2
- Shabalin, S.A. 2020. Assembly of dung beetles (Coleoptera: Scarabaeidae) – inhabitants of sheep dung in the south of Sikhote-Alin. *A.I. Kurentsov's Annual Memorial Meetings*, 31: 185–198. DOI: 10.25221/kurentzov.31.16 [In Russian]
- Shabalin, S.A. 2021. Assembly of dung beetles (Coleoptera, Scarabaeoidea) inhabiting sheep droppings in the northern spurs of the Manchurian-Korean Mountains (Russian Far East). *Contemporary Problems of Ecology*, 14(5): 500–514. DOI: 10.1134/S1995425521050140
- Shabalin, S.A. 2022a. Microstatal distribution of dung beetles (Coleoptera: Scarabaeoidea) in horse excrement in the southern Sikhote-Alin, Russia. *Contemporary Problems of Ecology*, 15(5): 475–483. DOI: 10.1134/S1995425522050110
- Shabalin, S.A. 2022b. Taxonomic diversity of the coprophilic scarab beetles (Coleoptera, Scarabaeoidea) in the southern part of Amur province of Palaearctic. *A.I. Kurentsov's Annual Memorial Meetings*, 33: 43–54. DOI: 10.25221/kurentzov.33.4 [In Russian]
- Shabalin, S.A. 2023. Estimation of biomass of dung beetles (Coleoptera: Scarabaeoidea) from the Russian Far East. *Far Eastern Entomologist*, 475: 17–30. DOI: 10.25221/fee.475.3
- Shabalin, S.A. 2024. Assembly of dung beetles (Coleoptera, Scarabaeoidea) inhabiting cow dung in the northern spurs of the Manchurian-Korean Mountains (Russian Far East). *Contemporary Problems of Ecology*, 17(2): 227–240. DOI: 10.1134/S1995425524020100
- Shabalin, S.A. 2025. Trophic connections of dung beetles (Coleoptera, Scarabaeoidea) in the Russian Far East. *A.I. Kurentsov's Annual Memorial Meetings*, 36: 55–67. DOI: 10.25221/kurentzov.36.5 [In Russian]
- Shabalin, S.A., Akhmetova, L.A., & Frolov, A.V. 2024. A new to Russia species of the genus *Aphodius* (Coleoptera, Scarabaeidae). *Far Eastern Entomologist*, 509: 7–10. DOI: 10.25221/fee.509.2
- Shabalin, S.A. & Berlov, E.Ya. 2008. A new to Russia species of the genus *Aphodius* (Coleoptera, Scarabaeidae). *Zoologicheskii Zhurnal*, 87(1): 122–123. [In Russian]
- Simmons, L.W., Ridsdill-Smith, T.J. (Ed.). 2011. *Ecology and Evolution of Dung Beetles.* Blackwell Publishing Ltd., 347 p.
- Spector, S. 2006. Scarabaeinae dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae): an invertebrate focal taxon for biodiversity research and conservation. *Coleopterists Bulletin. Monograph*, 5: 71–83.
- Tocco, C., Balmer, J.P., Villet, M.H. 2018. Trophic preference of southern African dung beetles (Scarabaeoidea: Scarabaeinae and Aphodiinae) and its influence on bioindicator surveys. *African Journal of Ecology*, 56(4): 938–948. DOI: 10.1111/aje.12523

- Yu, S.X. & Orlóci, L. 1990. On the niche overlap and its measurements. *Coenoses*, 5(3): 159–165.
- Ziani, S. & Bezděk, A. 2016. Tribe Onthophagini Burmeister, 1846. P. 180–204. In: Löbl, I., Löbl, D. (Ed.). *Catalogue of Palaearctic Coleoptera. Vol. 3. Scarabaeoidea – Scirtoidea – Dascilloidea – Buprestoidea – Byrrhoidea. Revised and Updated Edition*. Brill, Leiden, Boston.

© **Far Eastern entomologist (Far East. entomol.)** Journal published since October 1994.

Editor-in-Chief: S.Yu. Storozhenko

Editorial Board: A.S. Lelej, S.A. Belokobylskij, M.G. Ponomarenko, V.A. Mutin, E.A. Beljaev, E.A. Makarchenko, A.V. Gorochoy, T.M. Tiunova, M.Yu. Proshchalykin, S.A. Shabalin, V.M. Loktionov

Address: Federal Scientific Center of the East Asia Terrestrial Biodiversity (former Institute of Biology and Soil Science), Far East Branch of the Russian Academy of Sciences, 690022, Vladivostok-22, Russia.

E-mail: storozhenko@biosoil.ru

web-site: <http://www.biosoil.ru/fee>