

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 560: 1-16

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

October 2026

<https://doi.org/10.25221/fee.560.1>

<https://elibrary.ru/nsfany>

<https://zoobank.org/References/207B4EA2-E57B-499E-A859-BA0689834789>

ASSEMBLAGES OF DUNG BEETLES (COLEOPTERA, SCARABAEOIDEA) LIVING IN THE DUNG OF WILD ANIMALS IN RUSSIAN FAR EAST. COMMUNICATION 3. DUNG BEETLES INHABITAT IN THE DUNG OF TIGER (*PANTHERA TIGRIS*)

S. A. Shabalin

*Federal Scientific Center of the East Asia terrestrial biodiversity, Far Eastern Branch of
Russian Academy of Sciences, Vladivostok, 690022, Russia. E-mail: oxece-tonia@mail.ru*

Summary. In the south of the Russian Far East an assembly of dung beetles inhabiting tiger (*Panthera tigris*) dung has been studied. Data on the species composition, population dynamics, and number and biomass of the dung beetles are presented. A comparison of dung beetle assemblages inhabiting tiger, wild boar, and sika deer dung under identical spatiotemporal conditions, formed from a common species pool, reveals similar species compositions in these associations. However, their structure and the dynamic processes occurring within them differ significantly. This is reflected in a richer species composition and the number of species of individual functional groups in sika deer dung, differences in dominant species, seasonal distribution patterns of abundance and biomass (including peak values of these indicators for individual dung beetle functional groups), and aggregated overlapping temporal aspects of the ecological niches of coprophilous beetles. These differences are probably related to the size and structure of excrement of vertebrate animals, the presence of specific attractive substances in the droppings of carnivorous and omnivorous mammals.

Key words: dung beetles, assembly, seasonal dynamic, niches interception, biodiversity, Primorskii krai, Russian Far East.

С. А. Шабалин. Ассамблеи жуков-навозников (Coleoptera, Scarabaeoidea) обитающих в помете диких животных Дальнего Востока России. Сообщение 3. Навозники, обитающие в помете тигра (*Panthera tigris*) // Дальневосточный энтомолог. 2026. N 560. С. 1-16.

Резюме. На юге Дальнего Востока России изучена ассамблея навозников, обитающих в помете тигра (*Panthera tigris*). Приведены данные о видовом составе, динамике населения, численности и биомассе навозников. Сравнение ассамблей навозников, обитающих в помете тигра, кабана и пятнистого оленя в идентичных пространственно-временных условиях, и формирующихся на базе общего видового пула, показывает, что видовой состав этих ассоциаций сходен, однако особенности их структуры и динамические процессы, протекающие в них, имеют существенные различия. Это выражается в более богатом видовом составе и числе видов отдельных функциональных групп в помете пятнистого оленя, в различиях 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. Указанные различия, вероятно, связаны с размерами и строением экскрементов позвоночных животных, наличием специфических привлекающих веществ в помете хищных и всеядных млекопитающих.

INTRODUCTION

This publication is a completes the series devoted to the examination of dung beetle assemblages inhabiting the dung of wild animals in the Russian Far East. The assemblages of dung beetles living in the dung of wild animals on Russian Far East were examined only using the example of the sika deer (Shabalin, 2025a) and wild boar (Shabalin, 2026). We have considered only some assemblies of these beetles in dung some domestic animals, such as sheep, cow, and horse (Shabalin, 2020, 2021, 2022a, 2024). Beetles, inhabitants of the droppings of carnivorous animals such as tiger, have not previously been studied in this aspect. Accordingly, it is of interest to study the assemblage of dung beetles that inhabit tiger dung and compare it with that in sika deer, and wild boar dropping, 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 tiger dung in the Safari-park (south of Primorskii krai, Shkotovskii district) and compare the results with data previously obtained in the same locality and at the same time on the dung of sika deer (Shabalin, 2025a) and wild boar (Shabalin, 2026) to identify the features of the morphology and dynamics of the assemblies coprophages, determined by the type of droppings of mammals in Primorskii krai.

MATERIAL AND METHODS

The collection of beetles, both in tiger droppings, was carried out in the south of Primorskiy krai (Shkotovskiy 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 8, 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, 43.5 L of dung were removed and distilled and more than 1324 specimens 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 4.12, 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 1391 individuals of beetles belonging to 13 species were collected and identified, the list of which is given below.

Family Trogidae: *Trox (Trox) cadaverinus komareki* Balthasar, 1931, *Trox (Trox) ussuriensis* Balthasar, 1931.

Family Geotrupidae: *Phelotrupes (Chromogeotrupes) auratus* (Motschulsky, 1858).

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

Family Scarabaeidae, subfamily Aphodiinae: *Aphodaulacus koltzei* (Reitter, 1892), *Aphodaulacus nigrotessellatus* (Motschulsky, 1866), *Esymus pusillus* (Herbst, 1789), and *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 13.95 and 13.62 species; and the identified diversity was 93.18 and 95.45% of that theoretically expected, respectively. The share of identified species in the assembly of dung beetles inhabiting tiger dung in the Safari-park is 14.67% of the fauna of these beetles in the south of Sikhote-Alin Mountains (Shabalin, 2022b).

Coleoptera are classified into five 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 (3 species), in the groups of small size class, the medium size class, and large size dwellers only 2 species were recorded in each group.

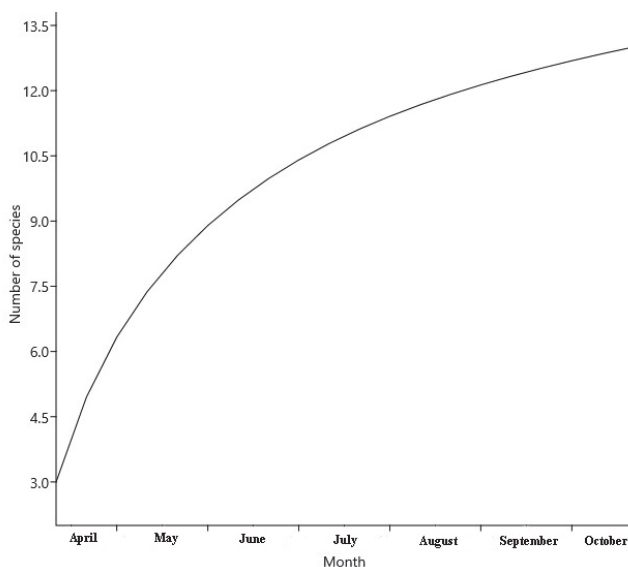


Fig. 1. Accumulation curve (Mao Tao) of dung beetle species.

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. From the first ten days of April to the first ten days of May small sized dweller *Aphodaulacus koltzei*, and medium sized dwellers (*Phaeaphodius rectus*, and *Aphodaulacus nigrotessellatus*) is found in the collections. In the second ten days of May, small sized dweller *Esymus pusillus*, large sized tunnelers *Onthophagus fodiens*, and medium sized tunnelers *Caccobius christophi* are added to it. From the first ten days of April to the second ten days of May, the number of species increases, from 1 to 6 species. The maximum taxonomic diversity of beetles inhabiting in the tiger dung in the Sikhote-Alin Mountains are noted in the second ten days of May and first ten days of June (6 species). From the second ten days of June a decrease in species diversity occurs. Thus, in this period only 1 – 2 species of dwellers and 1 – 4 species of tunnelers were activity. From the first ten days of August to second ten days of September, taxonomic diversity consists of tunnelers species with an extended period of adult activity (*Phelotrupes auratus*, *Caccobius christophi*, *C. brevis*, *Onthophagus atripennis*, *O. bivertex*, and *O. fodiens*). From the third ten days of September to the second ten days of October, diversity decreases sharply. In this period medium sized dweller *Phaeaphodius rectus*, and large sized tunnelers (*Onthophagus atripennis*, *Phelotrupes auratus*) were activity. In the third ten days of October, with a strong decrease in daytime temperatures, beetle activity stops (Fig. 2).

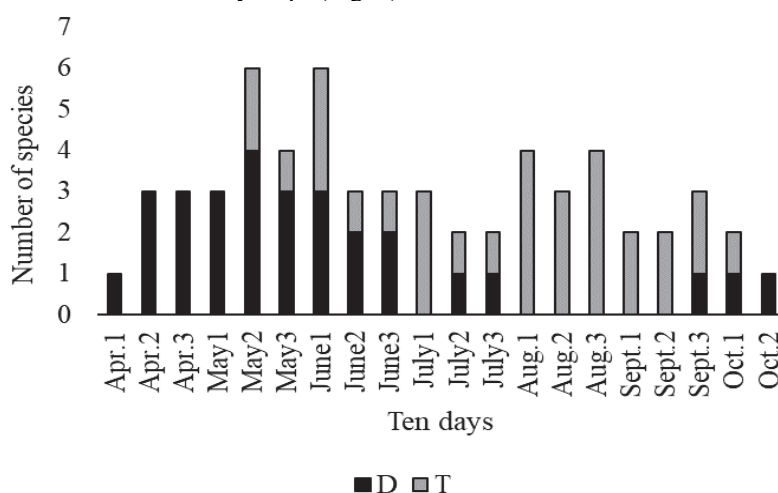


Fig. 2. Seasonal dynamics of the number of species. Trophodynamic groups: T – beetles making passages under a pile of substrate and storing provisions for the larvae, D – beetles living in the depth of manure.

Number and seasonal aspects of its changes. In the conditions of the Safari-Park, during the growing season, ne extended peak of increase in the number of coprophilous scarabaeoid beetles are observed in the tiger dung, with their number

exceeding 40 individuals / L. This significant, peak, with a total number of dung beetles of 43.82 – 61.14 individuals / L, falls on the second-third ten days of April (Table 1, 2). The peak is formed primarily due to the high performance of the small dweller *Aphodaulacus koltzei* (34.18 – 46.43 individuals / L).

Table 1. Number of dung beetles (specimens/L) in the tiger 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>	–	–	–	–	–	–	0,29	–	–	–
<i>C. christophi</i>	–	–	–	–	0,33	–	–	–	–	–
<i>O. uniformis</i>	–	–	–	–	–	–	0,57	–	–	–
<i>O. atripennis</i>	–	–	–	–	–	–	0,57	6,67	2,83	4,57
<i>O. bivertex</i>	–	–	–	–	–	0,18	–	–	–	0,57
<i>O. fodiens</i>	–	–	–	–	0,17	–	–	–	–	0,29
<i>A. koltzei</i>	0,33	46,43	34,18	11,11	30,17	7,64	1,43	0,33	–	–
<i>A. nigrotessellatus</i>	–	10,71	6,91	0,22	0,83	0,36	–	–	0,17	–
<i>E. pusillus</i>	–	–	–	–	1,17	–	0,57	–	–	–
<i>Ph. rectus</i>	–	4,00	2,73	0,44	5,83	0,73	0,29	0,33	0,17	–

Table 2. Number of dung beetles (specimens/L) in the tiger dung by ten-day periods (the second ten days of July – the first 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>T. cadaverinus</i>	–	0,11	–	–	–	–	–	–	–	–
<i>T. ussuriensis</i>	0,50	–	–	–	–	–	–	–	–	–
<i>Ph. auratus</i>	–	–	–	–	–	1,00	1,00	0,17	–	–
<i>C. christophi</i>	–	–	0,13	0,29	0,40	–	–	–	–	–
<i>C. brevis</i>	–	–	0,13	0,29	–	–	–	–	–	–
<i>O. atripennis</i>	12,50	8,89	1,25	3,14	8,40	2,00	2,00	0,17	0,50	–
<i>O. bivertex</i>	–	–	0,13	0,00	0,40	–	–	–	–	–
<i>O. fodiens</i>	–	–	–	–	0,40	–	–	–	–	–
<i>Ph. rectus</i>	–	–	–	–	–	–	–	1,17	23,00	0,40

The number of tunnelers during the growing season were quite low. Only in the second ten-day period of July was a slight increase observed, reaching 12.5 specimens / L, due to large sized *Onthophagus atripennis*. In this period accounts for 21.78 % of the total annual number of beetles of this group.

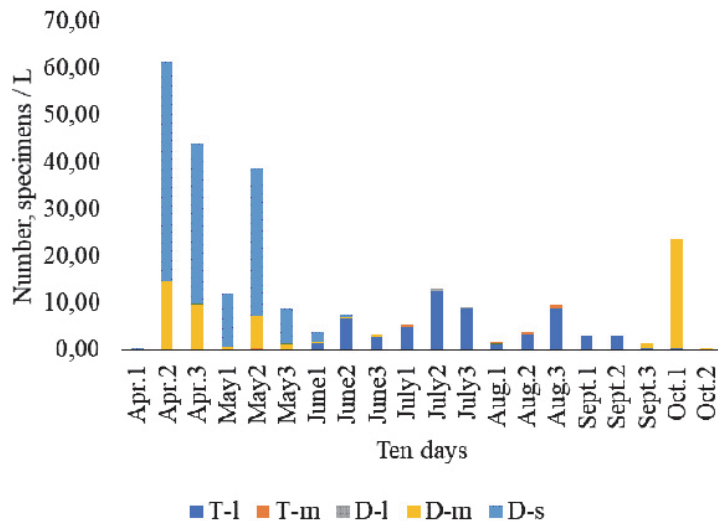


Fig. 3. Seasonal population dynamics. Trophodynamic groups: T – beetles making passages under a pile of substrate and storing provisions for the larvae; D – beetles living in the depth of manure. Size classes: m – medium; s – small.

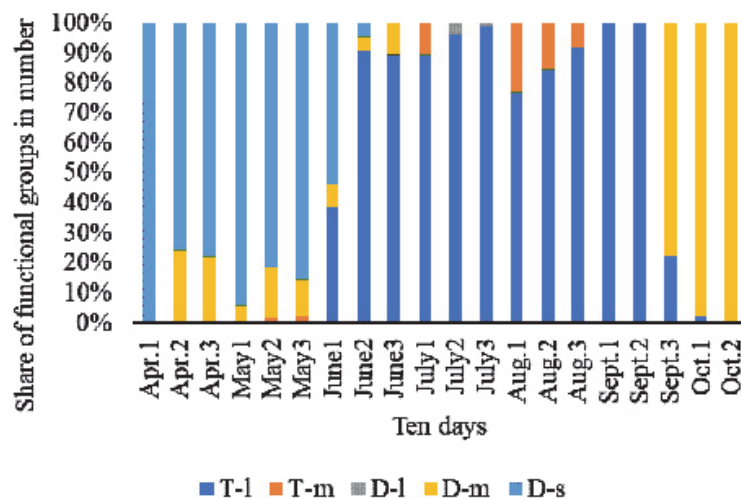


Fig. 4. Proportion of functional groups in the number of beetles. Designations of months and functional groups of beetles are the same as in fig. 3.

High numbers (more than 40 individuals / L) of dwellers were noted in the first-second ten days of April, which is 54.59% of their annual numbers, respectively (Table 1, 2). A significant share of the annual number of dwellers inhabiting in tiger dung in Sikhote-Alin Mountains falls on the periods from the first ten days of April to the third ten days of May (Fig. 3, 4). The functional group of large size dwellers did not have any pronounced peaks in numbers. For the functional group of dwellers of the medium size class, population peak was noted in the first ten days of October. This autumn peak in the number of medium sized dwellers is due to high rates of *Phaeaphodius rectus*. Small dwellers had one population peak. This peak was noted in the second-third ten days of April, and are associated with high numbers of *Aphodaulacus koltzei* (Table 1, 2).

Biomass and seasonal aspects of its changes. In the collection of beetles under consideration, three peaks in the rise in biomass values were noted in the second ten days of July, the second – third ten days of July, and the third ten days of August – the second ten days of September. All peaks are characterized by high values for large size tunnelers (Fig. 5, 6). These periods account for 9.56, 30.69, and 35.01% of their annual biomass respectively. These peaks are associated primarily with high biomass values in *Onthophagus atripennis* and *Phelotrupes auratus*.

The peaks rise in the biomass of medium sized tunnels were noted in the first ten days of July, and the third ten days of August; these periods accounts for 26.72 and 30.71% of their annual biomass, mainly due to high values of *Onthophagus bivertex* (Table 3, 4).

For small dwellers, increases in biomass indicators have been established in the second – third ten days of April. This peak account 58.55% 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 first ten days of October. This peak accounts for 46.57% of the annual biomass of beetles of this group. The peak of biomass in this group is associated with high rates of *Phaeaphodius rectus* (Table 3, 4). Biomass peaks for a large sized dweller are not expressed, since beetles of this group are represented by a limited number of specimens in a short time interval.

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 hyperbolic curve (Fig. 7). The resulting model with a sufficiently high coefficient of determination corresponds to a broken stick hypothesis. MacArthur's model assumes that niche space is divided into random, contiguous but non-overlapping regions (Whittaker, 1980).

Overlapping ecological niches. The overlap of temporal aspects of ecological niches for tunnelers in tiger dung in general, considering threshold values, was established for 5 pair of species (out of the maximum possible combination, 21 pairs), of species belong to the same size groups (23.81% of the maximum possible combination): *Ph. auratus* – *O. uniformis*, *C. christophi* – *C. brevis*, *C. christophi* – *O. bivertex*, *C. brevis* – *O. bivertex*, and *O. atripennis* – *O. fodiens*.

For dwellers, such an overlap of temporal aspects of ecological niches were obtained for 5 pairs of species out of the maximum possible combination of 9 pairs. Generations *Phaeaphodius rectus* divided into spring (s) and autumn (a). Considering the differentiation of beetles by size classes, 2 pairs of species are presented (22.22% of the maximum possible combination), for which there is a significant overlap of temporal aspects of ecological niches: *A. koltzei* – *E. pusillus*, and *A. nigrotessellatus* – *Ph. rectus* (s).

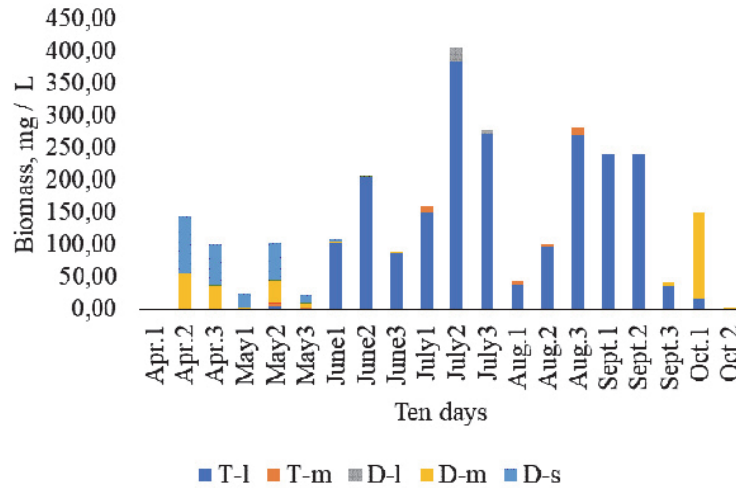


Fig. 5. Seasonal dynamics of biomass. Designations of months and functional groups of beetles are the same as in fig. 3.

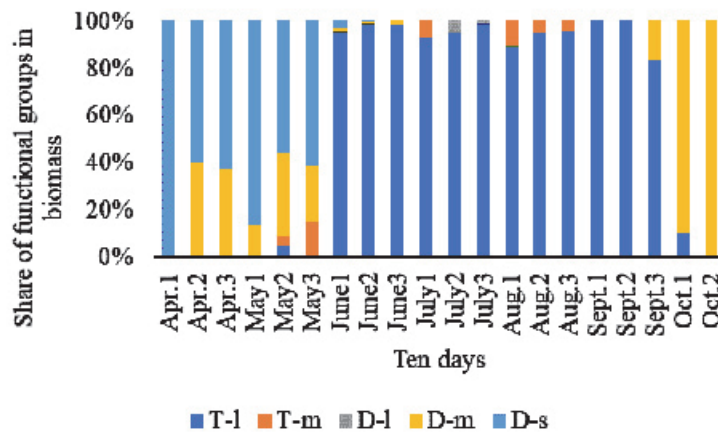


Fig. 6. Proportion of functional groups in biomass. Designations of months and functional groups of beetles are the same as in fig. 3.

Table 3. Dynamics of specific biomass of dung beetles (mg/L) in the tiger 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>	–	–	–	–	–	–	50,91	–	–	–
<i>C. christophi</i>	–	–	–	–	4,07	–	0,00	–	–	–
<i>O. uniformis</i>	–	–	–	–	–	–	34,54	–	–	–
<i>O. atripennis</i>	–	–	–	–	–	–	17,55	204,73	87,01	140,39
<i>O. bivertex</i>	–	–	–	–	–	3,46	–	–	–	10,86
<i>O. fodiens</i>	–	–	–	–	5,11	–	–	–	–	8,76
<i>A. koltzei</i>	0,62	85,89	63,24	20,56	55,81	14,13	2,64	0,62	–	–
<i>A. nigrotessellatus</i>	–	33,43	21,56	0,69	2,60	1,13	–	–	0,52	–
<i>E. pusillus</i>	–	–	–	–	1,49	–	0,73	–	–	–
<i>Ph. rectus</i>	–	23,28	15,87	2,59	33,95	4,23	1,66	1,94	0,97	–

Table 4. Dynamics of specific biomass of dung beetles (mg/L) in the tiger dung by ten-day periods (the second ten days of July – the first 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>T. cadaverinus</i>	–	3,63	–	–	–	–	–	–	–	–
<i>T. ussuriensis</i>	20,38	–	–	–	–	–	–	–	–	–
<i>Ph. auratus</i>	–	–	–	–	–	178,19	178,19	29,70	–	–
<i>C. christophi</i>	–	–	1,53	3,49	4,88	–	–	–	–	–
<i>C. brevis</i>	–	–	0,73	1,66	–	–	–	–	–	–
<i>O. atripennis</i>	383,88	272,98	38,39	96,52	257,96	61,42	61,42	5,12	15,36	–
<i>O. bivertex</i>	–	–	2,38	–	7,60	–	–	–	–	–
<i>O. fodiens</i>	–	–	–	–	12,26	–	–	–	–	–
<i>Ph. rectus</i>	–	–	–	–	–	–	–	6,79	133,86	2,33

DISCUSSION

The results obtained are the third in the Russian Far East to study the assemblages of dung beetles inhabiting in the dung of wild animals. The results allow us

to compare assemblages of dung beetles in sika deer (Shabalin, 2025a), wild boar (Shabalin, 2026), and tiger droppings, considering the fact that the observations were carried out in identical geographical conditions and time frames. In addition, it will allow us to examine the characteristics of the assemblages, given that the studies covered herbivorous, omnivorous, and carnivorous animal producers of manure. It should be noted that species of the family Geotrupidae previously noted in the droppings of sika deer were not found in the boar droppings, but the specialized keratophages species of the family Trogidae were noted only in tiger droppings. The assemblage of inhabitants of sika deer dung is more taxonomically diverse, with 14 species recorded, while in wild boar or tiger dung there are only 10 and 13 species, respectively. All species in wild boar droppings, with the exception of *Aphodaulacus nigrotessellatus*, were also noted in sika deer droppings. Tiger droppings contain the same species as sika deer droppings, with the exception of *Trox cadaverinus*, *Trox ussuriensis*, *Onthophagus fodiens*, and *Aphodaulacus nigrotessellatus*. The species composition of dung beetles found in boar or tiger dung is represented primarily by generalists. Only one species, *Aphodaulacus nigrotessellatus*, is a specialized inhabitant of carnivorous mammal dung. Perhaps the omnivorous nature of wild boars or carnivorous nature of tiger has led to the presence of special attractive components that attract this species of beetle. Hide beetles (Trogidae) find remains of wool in tiger droppings, which they eat. Strict trophic specialization is relatively rare in beetles of the Scarabaeidae and Trogidae families. Many species feed on both carrion and dung. Since rotting and digested animals are equally common, they can be used by members of the same species. This is the case with the necro-coprophagous Onthophagini, which we discovered

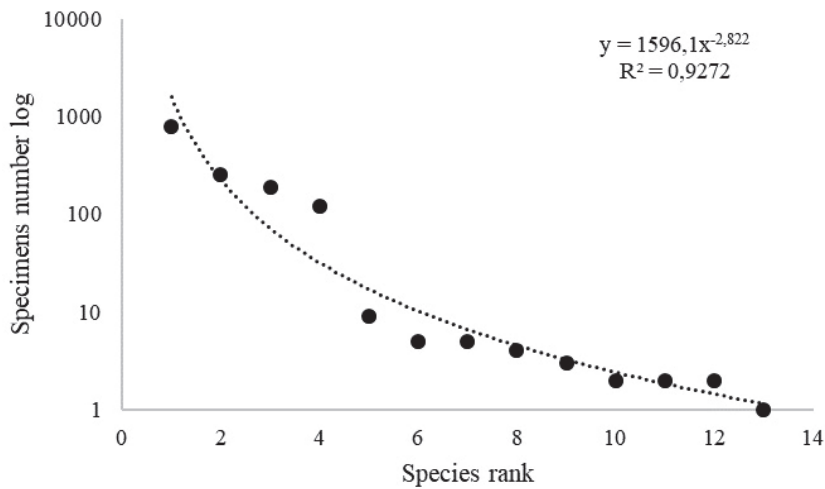


Fig. 7. Rank distribution of species.

in tiger dung. Necrophagous keratinivorous trogids may use tiger dung, as in the case of decomposing animal skins, by eating particles of wool. The wild boar droppings also show a low number of functional groups of beetles. Only 3, while the droppings of the sika deer or tiger contain 4 or 5 such groups. Large tunnels previously noted in sika deer droppings were not found in the boar droppings. Large dwellers were only observed in tiger dung. The obtained data on the population of beetles in local assemblages confirm the results of a previously conducted analysis of the food specialization of dung beetles in the Russian Far East (Shabalin, 2025b). Comparing the obtained results, it should be noted that the taxonomic diversity of all three assemblages examined is quite high. For example, only 12 dung beetle species were recorded from sika deer scat on the Japanese island of Honshu (Kanda et al., 2005). In the US state of Nebraska, which is not the tiger's native habitat, only two species of dung beetles were found in tiger droppings, while four species were found in wild boar droppings (Whipple, Hoback, 2012). The food specialization of dung beetles inhabiting in the droppings of wild animals in the Russian Far East are significantly poorer in species than the droppings of farm animals.

Beetles were observed in the droppings of wild boar, sika deer, and tiger from the beginning of April, but the activity of beetles in the droppings of sika deer and tiger continued until the second ten days of October, and in the droppings of wild boar only until the first ten days of the same month. The maximum species diversity in sika deer droppings was observed in the first and second ten days periods of July, while in wild boar droppings it peaked three ten days periods earlier, in the third ten days of May and the first ten days of June. The maximum species diversity in tiger droppings was found second ten days of May and first ten days of June. If in the droppings of a wild boar the onset of beetle activity is associated with two species *Phaeaphodius rectus*, and *Aphodaulacus koltzei*, then in the droppings of a sika deer and tiger the onset of beetle flight is associated exclusively with the latter species, and *Phaeaphodius rectus* appears only from the second – third ten days of April. It is noteworthy that the species diversity in wild boar and tiger droppings is low from the second ten days of June to October, compared to sika deer. In general, the maximum taxonomic diversity of dung beetles in both wild (Shabalin, 2025a, 2026) and agricultural (Shabalin, 2020, 2021, 2022b, 2024) animal droppings in the Sikhote-Alin Mountains occurs in late spring to mid-summer.

In general, peaks in the number of beetles in the assemblages under consideration occur mainly during different periods with fluctuations. So, if in sika deer droppings the spring peak in the number of beetles is falls on the second ten days of May, then in wild boar droppings springer peaks were observed on the first ten days of May, and on the third ten days May – first ten days of June, however in tiger droppings this peak was observed on the second-third ten days of April. The summer peak in wild boar droppings was noted in the first ten days of July, in sika deer and tiger droppings this peak was not observed. In addition, these peaks, although formed mainly due to the high number of dwellers, are due to increases in the numbers of predominantly same species in the spring. However, summer peak expressed in wild boar droppings is associated with a high number of small sized dwellers *Labarrus sublimbatus*. This species has been observed in sika deer droppings, and was not noted at all in the tiger's litter.

The peak in the number of medium sized tunnelers in all assemblies under consideration occurs in August and is associated with *Caccobius christophi*. As for tiger droppings, this species was also observed in this substrate in August, but had a rather low abundance here, not exceeding 0.4 specimens per liter. The peaks in the numbers of both medium sized and small dwellers differ in number and occur in different periods, and are due to increases in the numbers of predominantly different species. Thus, in sika deer droppings, the spring peak in the number of medium sized dweller is associated with *Agrilinus ater*, and the autumn peak with *Phaeaphodius rectus*, in wild boar droppings, the spring peak is associated with the latter species, but the autumn peak is not represented at all. In tiger droppings, the spring peak in the number of medium sized dweller is not represented, but the autumn peak in the first ten days of October is associated with *Phaeaphodius rectus*. As for small sized dwellers, the spring peak in sika deer droppings is associated with *Esymus pusillus*, and *Aphodaulacus koltzei*, while the summer peak is not present at all. Similar features were noted for tiger droppings, however, the peak in numbers was associated primarily with the latter species, and *Esymus pusillus* had a rather low number. In wild boar droppings, the spring peak is associated with *Aphodaulacus koltzei*, while the summer peak is associated with *Labarrus sublimbatus*.

The biomass of beetles living in dung of wild boar, sika deer and tiger is characterized by peak values at approximately the in different time. The presence of a functional group of large tunnelers in the sika deer and tiger droppings has a significant impact on this. Thus, peak biomass levels in sika deer dung occur exclusively in the second ten days of July and are associated with large tunnelers, but in tiger dung in the second ten days of July, in the second – third ten days of July, and the third ten days of August – the second ten days of September and also are associated with large tunnelers. On the contrary, in the droppings of wild boar peaks biomass levels occur in the first ten days of May, the third ten days of May – first ten days of June, and the first ten days of July and are associated with small and medium size dwellers. While the peak biomass values of medium sized tunnelers and small sized dwellers are approximately the same, differing only by ten days and associated with the same species in both wild boar and sika deer droppings, the peak biomass values of medium sized dwellers have significant differences. Thus, the spring peak in the biomass of medium sized dwellers in wild boar droppings occurs at the third ten days of May – first ten days of June and is associated with *Phaeaphodius rectus*, but in sika deer droppings this period occurs at the second ten days of May, and associated with *Acrossus superatratatus*, and *Agrilinus ater*, but in tiger droppings this period occurs at the first ten days of October and was associated with high rates of *Phaeaphodius rectus*. At the same time, the autumn peak of biomass indicators of medium sized dwellers in wild boar droppings is not expressed at all. Such differences in peak biomass values cannot be attributed to local weather or geographic conditions, since beetle collections were carried out in a single location. It is likely that the above-mentioned features of biomass peaks are due to the peculiarities of the development cycles of beetles and their seasonal selectivity in the choice of food objects.

The rank distribution of species in the assemblies of sika deer and wild boar dung corresponds to a geometric series or niche interception hypothesis, but in tiger dung corresponds to a broken stick hypothesis. The overlap of the temporal aspects of the ecological niches of dung beetles in the sika deer and tiger dung assemblages is generally comparable, but for the wild boar dung assemblage, a slight increase in this indicator is noted.

The above comparisons of dung beetle assemblies inhabiting in dung of wild boar, tiger, 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 wild boar 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), the presence of specific keratophages in tiger droppings, and aggregate indicators of the overlap of temporal aspects of ecological niches of coprophilous scarabaeoid beetles. Apparently, these differences are due to a number of factors, among which we should note the anatomy and structure of the digestive system of vertebrates and type of animal nutrition (carnivore, omnivore and herbivore) that produce dung. It is known that water content, carbon/nitrogen ratio, amino acid, neutral lipid fatty acid, free fatty acid and sterol composition and concentrations in dung have a serious difference, depending on the type of vertebrate animal (Frank *et al.*, 2017). In addition, dung volatiles clearly differed among mammal's species, allowing olfactory discrimination by dung beetles (Dormont *et al.*, 2007; Scholtz *et al.*, 2009; Dormont *et al.*, 2010). The morphology of the dung of some vertebrate animals also differs significantly in both volume and shape (Chame, 2003), which creates conditions for different evaporation of water from the surface of dung.

CONCLUSIONS

Comparisons of assemblies of dung beetles that inhabit tiger, wild boar and sika deer dung in identical spatiotemporal conditions and form on the basis of a common pool of species show that the species composition of these assemblies is similar, but their structural features 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 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. The above differences are probably associated with the size and structure of excrement of vertebrate animals, the presence of specific attracting substances in wild boar droppings associated with omnivorousness and in tiger droppings associated with predatoriness. The morphology of the dung of consideration vertebrate animals also differs significantly in both volume and shape, which creates conditions for different evaporation of water from the surface of dung.

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. 1.* Nauka, Leningrad. [In Russian]
- Chame, M. 2003. Terrestrial Mammal Feces: A Morphometric Summary and Description. *Memórias do Instituto Oswaldo Cruz*, 98(Suppl 1): 71–94. DOI: 10.1590/S0074-02762003000900014.
- 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.
- Dormont, L., Rapior, S., McKey, D.B., Lumaret, J.P. 2007. Influence of dung volatiles on the process of resource selection by coprophagous beetles. *Chemoecology*, 17: 23–30. DOI: 10.1007/s00049-006-0355-7
- Dormont, L., Jay-Robert, P., Bessiere, J.M., Rapior, S., Lumaret, J.P. 2010. Innate olfactory preferences in dung beetles. *Journal of Experimental Biology*, 213: 3177–3186. DOI: 10.1242/jeb.040964
- Frank, K., Brückner, A., Hilpert, A., Heethoff, M., Blüthgen, N. 2017. Nutrient quality of vertebrate dung as a diet for dung beetles. *Scientific Reports*, 7: 12141. DOI: 10.1038/s41598-017-12265-y
- Hanski I., Cambefort Y. (Ed.). 1991. *Dung beetle ecology*. Princeton University Press, Princeton, New Jersey. 481 pp.
- 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]
- Kanda, N., Yokota, T., Shibata, E., Sato, H. 2005. Diversity of dung-beetle community in declining Japanese subalpine forest caused by an increasing sika deer population. *Ecological Research*, 20: 135–141. DOI: 10.1007/s11284-004-0033-6
- 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.
- Scholtz, C.H., Davis, A.L.V. & Kryger, U. 2009. *Evolutionary biology and conservation of dung beetles*. Pensoft Publishers, Sofia. 567 pp.
- 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. 2025a. 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*). *Far Eastern Entomologist*, 532: 1–16. DOI: 10.25221/fee.532.1
- Shabalin, S.A. 2025b. 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. 2026. Assemblages of dung beetles (Coleoptera, Scarabaeoidea) living in the dung of wild animals in the Russian Far East. Communication 2. Inhabitants of the dung of the wild boar (*Sus scrofa*). *Far Eastern Entomologist*, 532: 1–16. DOI: 10.25221/fee.532.1
- 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]
- Whipple, S.D., Hoback, W.W. 2012. A Comparison of Dung Beetle (Coleoptera: Scarabaeidae) Attraction to Native and Exotic Mammal Dung. *Environmental Entomology*, 41(2): 238–244. DOI: 10.1603/EN11285
- Whittaker, R.H. 1975. *Communities and Ecosystems*. New York: MacMillan Publishing Co. 385 p.
- Yu, S.X., Orlóci, L. 1990. On the niche overlap and its measurements. *Coenoses*, 5(3): 159–165.
- Ziani, S., Bezdek, 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.