

Seasonal population dynamics of Diptera families in deciduous forests of Central European Russia

Mikhail Esin, and Alexander Ruchin*

Mordovia State Nature Reserve and National Park «Smolny», 430005 Saransk, Russia

Abstract. Seasonal rhythms have been found in practically all groups of insects, but in Diptera they have been studied to a lesser extent. In deciduous forests of the European part of Russia (Republic of Mordovia, Temnikov district) seasonal dynamics of Diptera abundance was studied in 9 families (Tipulidae, Lonchaeidae, Aulacigastridae, Milichiidae, Heleomyzidae, Anthomyiidae, Muscidae, Fanniidae, Calliphoridae). Two peaks in seasonal abundance dynamics were characteristic of Tipulidae, Heleomyzidae, Fanniidae. Anthomyiidae had one peak in early June. Milichiidae had one peak in July. Muscidae had one peak in mid-August. Lonchaeidae and Aulacigastridae had a three-peak pattern with the highest abundance in June. Calliphoridae experienced a gradual increase in abundance from June and had a peak in early September. Numbers of *Phaonia pallida* (Muscidae) were at a minimum in June at different heights from the soil surface and gradually increased with peaks in August and September. The first individuals of *Thricops simplex* (Muscidae) did not appear in the traps until the first half of July. Thereafter its numbers increased very rapidly and reached a maximum in early September.

1 Introduction

In temperate latitudes, the year is divided into seasons, which differ in the values of abiotic environmental factors (duration of daylight hours, air, water and soil temperatures, amount of precipitation). This leads to annual rhythmicity in behavior, reproduction, individual development and physiological processes of animals [1–5]. The variability of climatic parameters in recent years causes changes in the ranges of species, their distribution in the latitudinal direction [6–9]. In addition to range changes, there is another well-studied insect response to climate change - changes in phenology. Phenological studies are now actively developing [10, 11]. Ongoing climate change as well as the need to assess the significance of these changes for natural communities, crops and forestry facilitate the process [12, 13]. The dynamic nature of species and community abundance in ecosystems can provide insight into temporal changes in communities in different seasons. At the same time, many parameters of biology and ecology of organisms (reproduction, emergence of adults, etc.) are determined. Identifying the factors underlying changes in phenology is crucial for

* Corresponding author: ruchin.alexander@gmail.com

understanding the effects of global climate change [14–16]. In this case, insect communities provide models for tracking phenological shifts in species abundance, as temperature fluctuations and resource availability influence a lot their physiology [14, 17, 18].

Seasonal rhythms have been identified in almost all insect groups, in particular Coleoptera, Lepidoptera, Hymenoptera and others [19–27]. The order Diptera is the least studied of the most numerous groups of insects. Of particular interest is the seasonal dynamics of Diptera abundance in natural habitats. Seasonal population dynamics of individual Diptera families differed in five biotopes. The autumn increase in abundance in all biotopes exceeded the summer peak by several times [28]. Peaks of Tephritidae abundance were recorded from February to October, coinciding with the phenological stages of fruit bearing, ripening and harvesting [29]. In the Czech Republic, since mid-April there has been a sharp increase in the occurrence of mosquito species caused by melting snow. They peaked in early May, but gradually stopped flying in June [30]. Seasonal Tabanidae activity in France showed two peaks in abundance, one in late May with some species and one in late August with other species [31].

The objectives of the study were (1) to investigate the seasonal dynamics of individual Diptera families at different altitudes in deciduous forests and (2) to study the seasonal dynamics of two Mucosidae species.

2 Materials and methods

The research was carried out in the Republic of Mordovia (European part of Russia, Mordovia State Nature Reserve). The Mordovia State Nature Reserve covers an area of 321.62 km². Forest ecosystems cover 89.3% of the whole area. The territory of the Mordovia State Nature Reserve is part of a zone of coniferous-broadleaved forests on the border with the forest-steppe.

The field survey has been carried out in the deciduous forest, consisted of *Tilia cordata* (90% of the forest canopy layer) and *Quercus robur* (10%) with the projective cover of 60%. Understory layer (projective cover: 70%) is represented by *Acer platanoides* (projective cover: 65%), *Ulmus glabra* (10%), *Tilia cordata* (40%), *Euonymus verrucosus* (solitary plants). Ground layer (projective cover: 85%) consists of *Carex pilosa* (projective cover: 70%), *Mercurialis perennis* (5%), *Glechoma hederacea* (2%), *Asarum europaeum* (1%). Other species have projective cover of less than 1%: *Aegopodium podagraria*, *Milium effusum*, *Stachys sylvatica*, *Aconitum septentrionalis*, *Viola mirabilis*, *Polygonatum multiflorum* (Liliaceae), *Pulmonaria obscura*, *Geum urbanum*, *Lathyrus vernus*, *Rubus holostea*, *Rubus saxatilis*, *Equisetum sylvaticus*, *Dryopteris filix-mas*, *Paris quadrifolia*, *Galium odoratum*, *Anthriscus sylvestris*.

Diptera were collected from June to September 2020. In each forest fragment 4 sampling traps were set at different heights: the forest layer close to the soil surface and grass – 1.5 m from the soil surface, the undergrowth and shrub layer – 3.5 m from the soil surface, the lower canopy layer – 7.5 m from the soil surface, the upper canopy layer – 12 m from the soil surface. Traps were placed on tree branches. To avoid possible marginal effects, the traps were placed inside forest patches. In total there were four such fragments of deciduous forest. Each forest patch was located more than 1.5 km away from the other. Thus, these plots represented individual forest fragments. The total sampling effort amounted to 144 trap exposures with nine repeats at each height.

All collections were made with traps of simple design. Beer was used as bait. Sugar was added for digestion [32]. The collected samples were transported in plastic bags containing 70% alcohol from the forest to the laboratory. Samples were sorted and identified in the laboratory. Sample identification was carried out using a reference book [33].

3 Results

More than 58,000 specimens and 26 Diptera families were collected and identified. The maximum number of specimens of all Diptera was captured at 1.5 m, the minimum at 3.5 m in the undergrowth. In the upper canopy the number of Diptera was second highest. More than 1000 specimens (total for the season) in traps were represented by the following families: Tipulidae, Anisopodidae, Lonchaeidae, Milichiidae, Drosophilidae, Fanniidae, Muscidae, Calliphoridae. Drosophilidae was the most abundant (49.3% of the total number of specimens). Numbers of 11 families (Tabanidae, Phoridae, Ulidiidae, Platystomatidae, Pallopteridae, Piophilidae, Lauxaniidae, Odiinidae, Chloropidae, Scathophagidae, Sarcophagidae, Tachinidae) were below 100 specimens per season. The other families had 100 to 1000 specimens in traps.

We traced seasonal abundance dynamics at different altitudes in deciduous forests in nine families whose total abundance for the season was high enough for analysis. The seasonal abundance cycle for Tipulidae was two-peak (Figure 1). A small peak in abundance was observed in early June and the highest peak was recorded in mid-August.

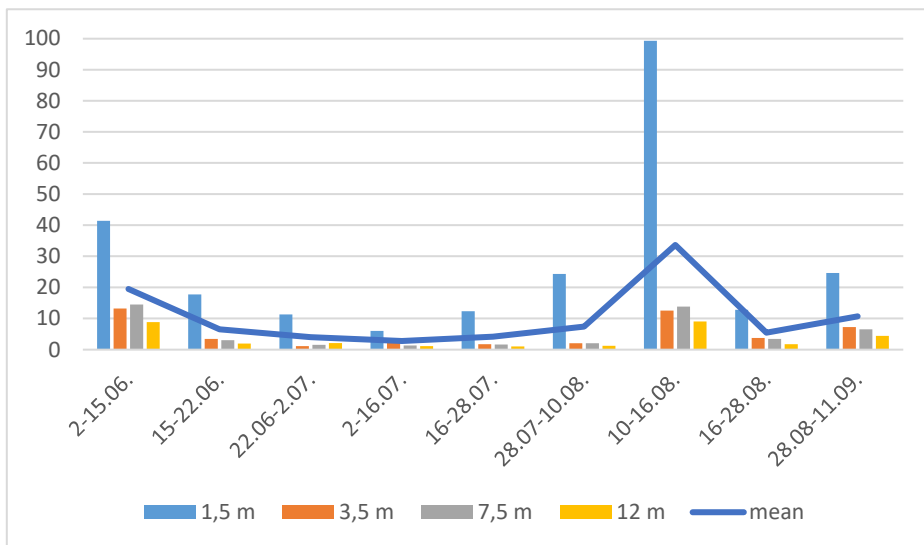


Fig. 1. Seasonal dynamics of Tipulidae abundance at different heights in temperate deciduous forest (ordinate axis - specimen/day).

Tipulidae was the most abundant at 1.5 m. Numbers of Lonchaeidae were higher during the season in June, late July and the second half of August (Figure 2). The most abundant individuals of this family were at a height of 12 m.

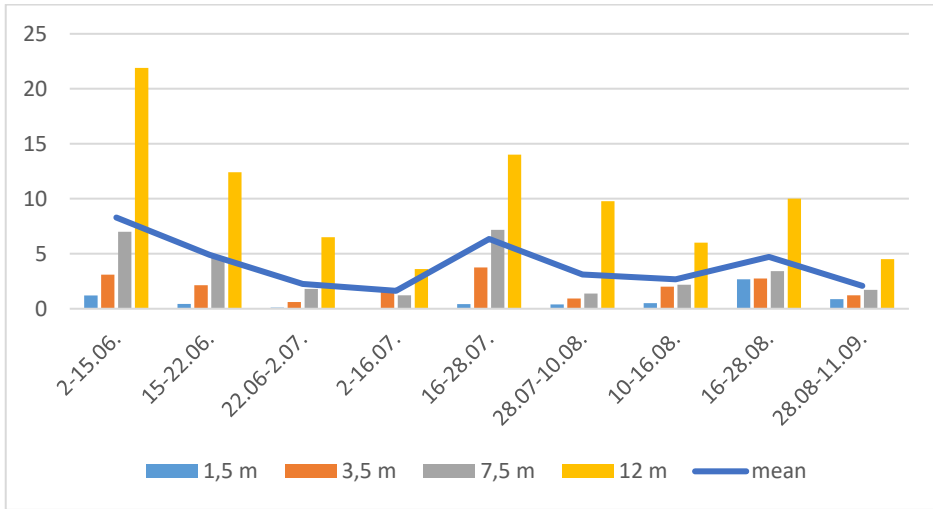


Fig. 2. Seasonal dynamics of Lonchaeidae abundance at different altitudes in temperate deciduous forest (ordinate axis - specimen/day).

Numbers of Aulacigastridae during the season were also higher in June, late July and the second half of August (Figure 3).

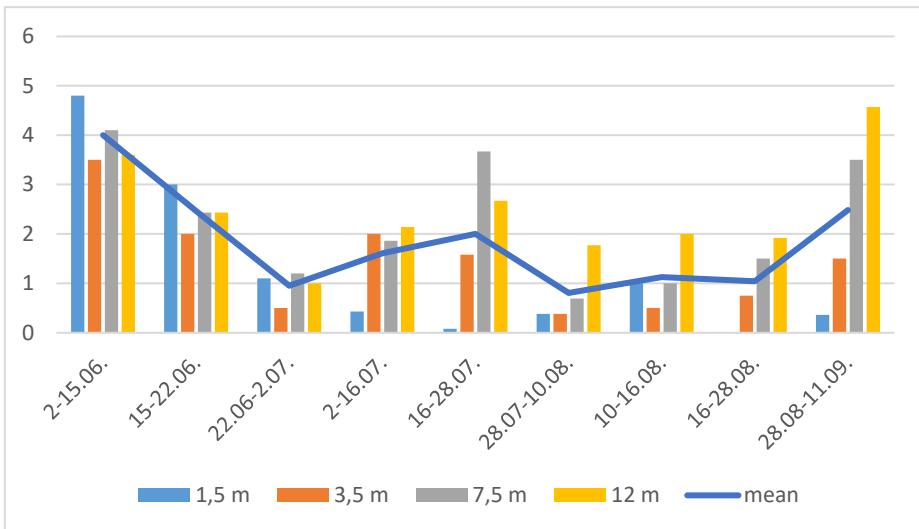


Fig. 3. Seasonal dynamics of Aulacigastridae abundance at different altitudes in a deciduous forest in the temperate zone (ordinate axis - specimen/day).

The family Milichiidae had one significant increase in abundance in July (Figure 4).

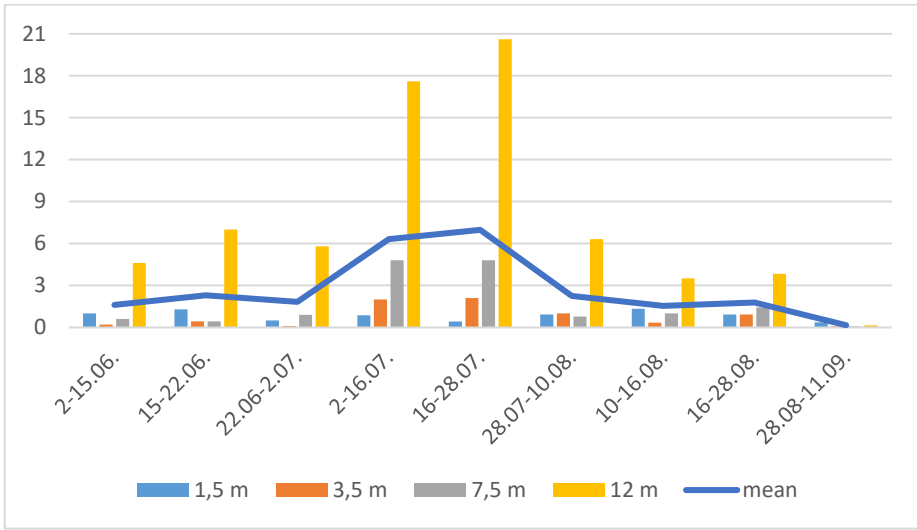


Fig. 4. Seasonal dynamics of Milichiidae abundance at different altitudes in temperate deciduous forest (ordinate axis - specimen/day).

The seasonal dynamics of Heleomyzidae abundance were two-peak, with peaks in early June and late August (Figure 5).

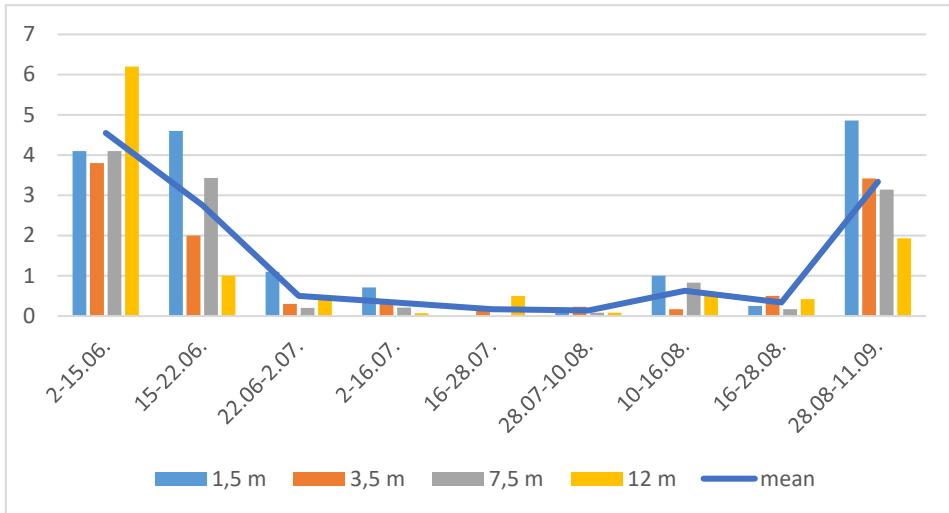


Fig. 5. Seasonal dynamics of Heleomyzidae abundance at different altitudes in temperate deciduous forest (ordinate axis - specimen/day).

The average abundance of Anthomyiidae at the beginning of June was many times higher than on subsequent sampling dates. Therefore, despite small increases in abundance in mid-July and mid-August, it is possible to say that the abundance of this family is single-peak (Figure 6).

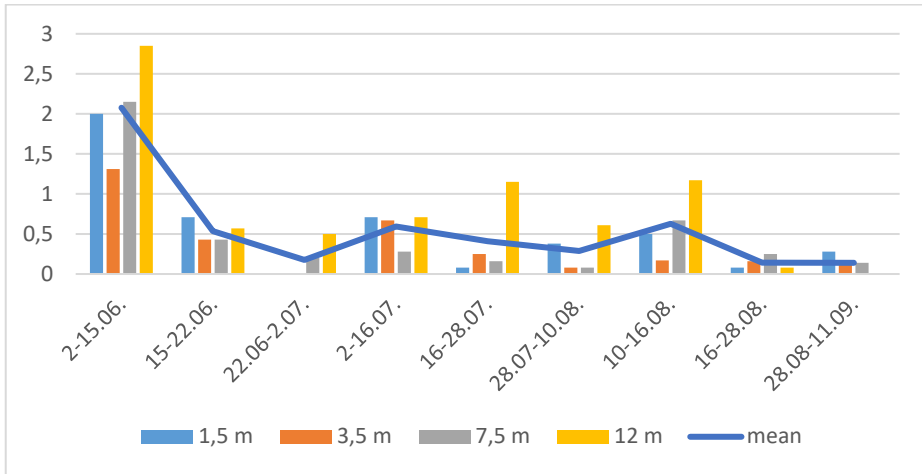


Fig. 6. Seasonal population dynamics of Anthomyiidae at different altitudes in temperate deciduous forest (ordinate axis - specimen/day).

The family Fanniidae had two-peak cyclicality of abundance. The first increase in abundance was obtained in the second half of July and the second more significant one in mid-August (Figure 7).

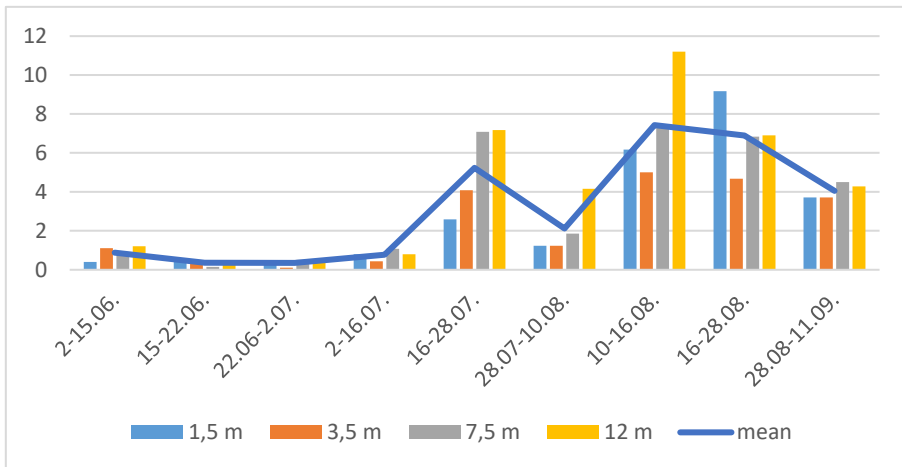


Fig. 7. Seasonal population dynamics of Fanniidae at different altitudes in temperate deciduous forest (ordinate axis - specimen/day).

Muscidae had one peak in mid-August (Figure 8). In early June the abundance of this family was very low in all traps.

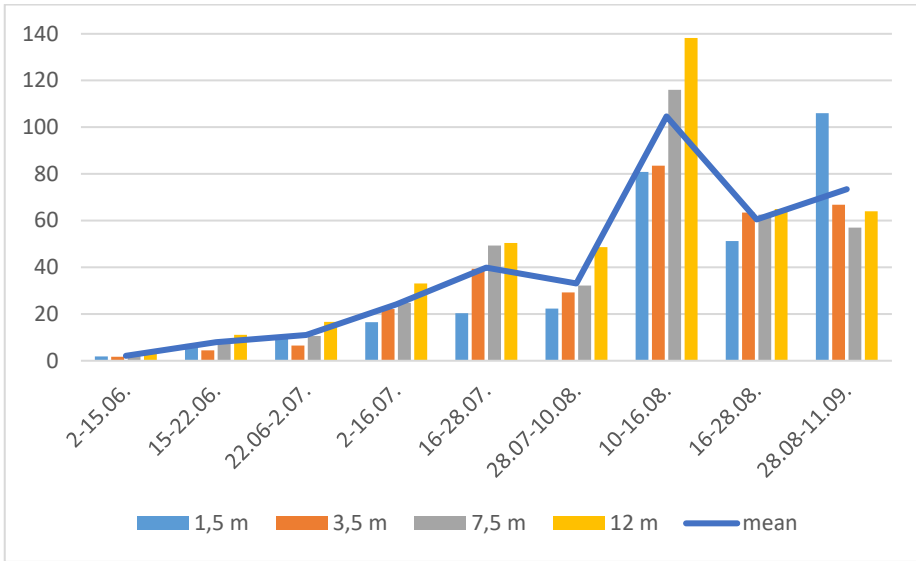


Fig. 8. Seasonal dynamics of Muscidae abundance at different altitudes in temperate deciduous forest (ordinate axis - specimen/day).

The family Calliphoridae was characterized by a gradual increase in abundance from June and peaked in early September (Figure 9).

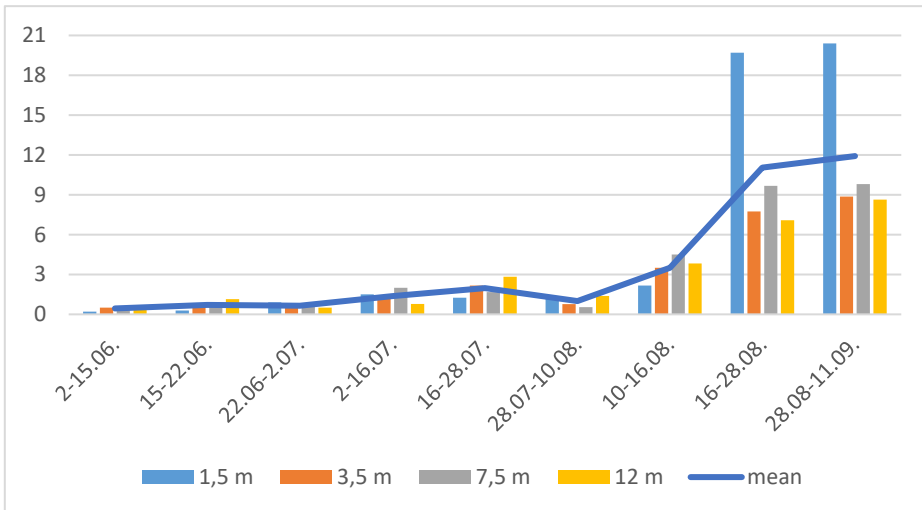


Fig. 9. Seasonal dynamics of abundance of Calliphoridae at different altitudes in temperate deciduous forest (ordinate axis - specimen/day).

The Muscidae family was second after the Drosophilidae in terms of the total number of individuals. The total abundance was almost identical at all altitudes. However, differences were present at the level of individual species. For example, the two species *Phaonia pallida* and *Thricops simplex* dominated in abundance in the samples (Figure 10 and 11).

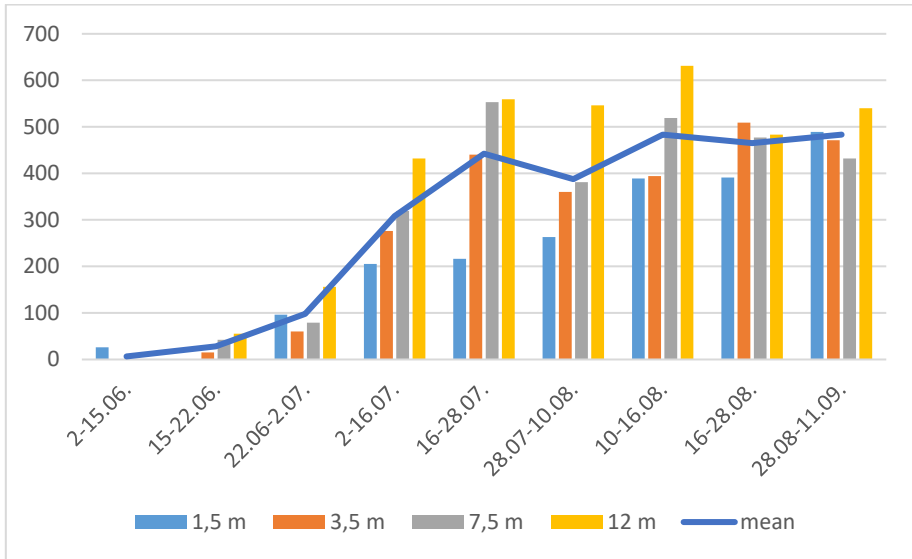


Fig. 10. Seasonal dynamics of *Phaonia pallida* (Muscidae) abundance at different heights in temperate deciduous forest (ordinate axis - specimen/day).

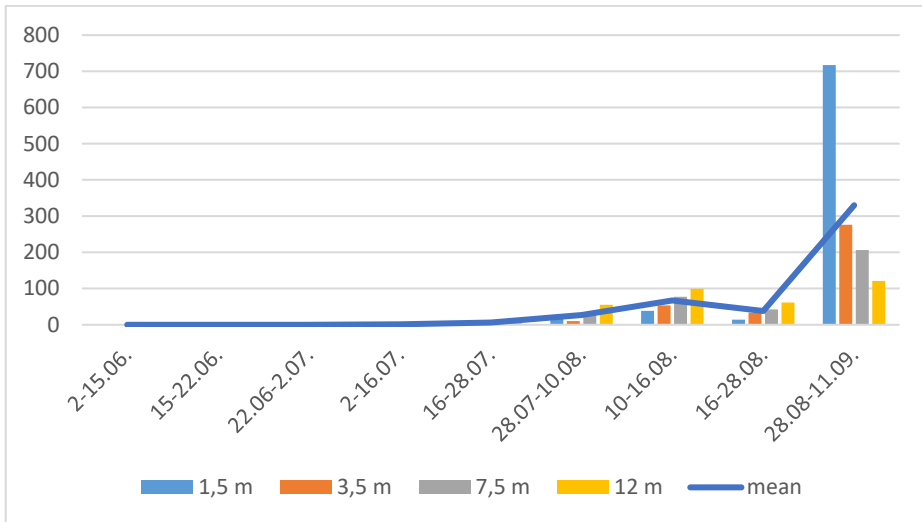


Fig. 11. Seasonal dynamics of *Thricops simplex* (Muscidae) abundance at different heights in temperate deciduous forest (ordinate axis - specimen/day).

Numbers of *Phaonia pallida* in June at different heights from the soil surface were at a minimum and gradually increased. The maximum numbers were recorded in August and September. However, the maximum abundance of this species was obtained in the tree crowns. In contrast, *Thricops simplex* was most abundant close to the soil surface. The first individuals of this species did not appear in the traps until the first half of July. Thereafter its abundance increased very rapidly and reached a maximum in early September.

4 Discussion

Our study provides an insight into the seasonal dynamics of Diptera sampled using beer traps set at different altitudes in deciduous forests of the temperate zone of European Russia. Traps were set in May, but the first Diptera individuals were captured only in early June. Seasonal cycles of Diptera abundance are related to seasonal changes in temperature, day length, humidity and other factors. Water levels and moisture regime influence seasonal activity of aquatic breeding species [28, 34–40].

In our study, the seasonal cycle of abundance in Tipulidae was two-peak, with peaks in early June and mid-August. Hernández-Ortiz et al. [39] obtained a single-peak pattern in Tipulidae abundance in the tropics. In the forests of Massachusetts (USA), this family has a two-peak pattern with peaks in August and September [34].

Species of the family Lonchaeidae are associated in their life cycle with their breeding sites (living or decaying plant organisms, including grasses and trees). The larvae of some species live under the bark of dead or dying deciduous and coniferous trees. This relationship accounts for their seasonal dynamics [41–43]. It is possible that the three-vertebrate dynamics just depend on larval feeding sites, emergence, flowering and so on.

Numbers of species of the family Aulacigastridae were also higher during the season in June, late July and the second half of August. The larvae of Aulacigastridae develop in the leaking sap on the bark of various trees and adult flies can be found sitting along them [44]. In Central Europe, all Aulacigaster species give birth to two generations annually and adults of the second generation overwinter in tree hollows [44]. The family Milichiidae had one significant maximum abundance in July. The larvae of Milichiidae feed on decaying materials of plant and animal origin. They are found under the bark of trees damaged by other insects [45, 46].

The seasonal dynamics of Heleomyzidae abundance was two-peak, with peaks in early June and late August. Many members of this family are adapted to the cold and abundant in the mountains and in the north. Heleomyzidae are one of the most common groups of insects active in winter. Many species are most active in the evening and autumn months [47].

Numbers of Anthomyiidae in early June were many times higher than at later sampling dates, especially in tree crowns. The larvae of Anthomyiidae species are mainly phytophagous, saprophagous or omnivorous. The emergence of adults is related to the vegetation dynamics of Anthomyiidae larvae [48]. We are not aware of any publications on Anthomyiidae whose larvae may live in foliage, branches or in the trunks of deciduous trees. However, the life cycle of one species (*Strobilomyia appalachensis*), whose larvae feed on pine cones and whose range includes temperate zones of Canada [49] is described. Adults of *Strobilomyia appalachensis* are caught near tree cones in May and early June. Eggs are laid between the scales of seed cones in early June, starting when the scales on most cones have been closed and ending one week after the cones have been fully hung. The larvae feed on the buds, moult and then drop out into the soil. Larval deposition occurs from late June to late July and largely correlates with periods of rainfall. Mature larvae move into the soil and overwinter in the soil as pupae. Adults appear in spring [49]. It is possible that similar life cycles of local species are similar to the Canadian species. For example, Anthomyiidae dominate in Czech forests in spring [50]. The family Fanniidae has a two-peak abundance cycle, with a greater increase in abundance in mid-August. Similar data were obtained in the Bavarian Forest [50].

For Muscidae, a single abundance peak was obtained in mid-August. Previously [28], two main population peaks of this family were recorded in different habitats. The largest autumn peak was obtained in the first half of October. However, there were two other small increases in trap abundance of this family in the second half of July and in late August. It is likely that species of this family are actively preparing for wintering and show high activity at

moderately high temperatures [28]. It is possible that in our studies in deciduous forests in September and October we could have seen a similar increase in numbers, but the experiments were terminated in the middle of September. The family Calliphoridae showed a gradual increase in numbers from June and a peak in early September. A similar relationship was obtained earlier in other biotopes in the forests of central European Russia [28].

Phaonia pallida abundance gradually increased during the season and peaked in September. Similar data were previously reported by Martin-Vega and Baz [51]. *Thricops simplex* was most abundantly caught close to the soil surface. Its abundance increased very rapidly in the traps from late July and peaked in early September. The larvae of *Thricops simplex* inhabit animal excreta, decomposing fallen matter, and decaying fungi [50, 52, 53]. Its maximum abundance has been reported in summer [50]. It is possible that in our study adults were actively flying to the bait.

5 Conclusion

Analysis of seasonal dynamics showed that for 9 Diptera families (Tipulidae, Lonchaeidae, Aulacigastridae, Milichiidae, Heleomyzidae, Anthomyiidae, Muscidae, Fanniidae, Calliphoridae) it is specific. Some families had bimodal dynamics (Tipulidae, Heleomyzidae, Fanniidae), other families had only one significant peak in abundance (Anthomyiidae, Milichiidae, Muscidae, Calliphoridae), or abundance dynamics with a few increases during the season (Lonchaeidae, Aulacigastridae). Our results indicate a significant role of Diptera in seasonal changes in the number of insect communities in deciduous forests, and this may influence the dynamic processes of nutrient cycling in these forests.

This research was funded by the Russian Science Foundation, grant number 22-14-00026.

References

1. B. J. McGill, B. J. Enquist, E. Weiher, M. Westoby, Trends Ecol. Evol. **21(4)**, 178-185 (2006). <https://doi.org/10.1016/j.tree.2006.02.002>
2. P. Lehmann, W. S. Van Der Bijl, C. Nylin, W. Wheat, K. Gotthard, Physiol. Entomol. **42**, 232-238 (2017)
3. B. Chhetri, H. K. Badola, Barat S. Nat. Cons. Res. **6(3)**, 87-96 (2021). <https://dx.doi.org/10.24189/ncr.2021.040>
4. M. B. Nosova, E. D. Lapshina, A. A. Notov, M. S. Ignatov, Nat. Cons. Res. **7(1)**, 80-95 (2022). <https://dx.doi.org/10.24189/ncr.2022.010>
5. S. S. Shinkarenko, Nat. Cons. Res. **7(3)**, 26-45 (2022). <https://dx.doi.org/10.24189/ncr.2022.028>
6. C. Parmesan, G. Yohe, Nature **521**, 37-42 (2003)
7. K. Tougeron, Entomol. Experim. Appl. **167**, 27-36 (2019)
8. O. N. Lipka, S. V. Krylenko, Proc. Mord. State Nat. Res. **28**, 130-144 (2021)
9. M. P. Shashkov, M. V. Bobrovsky, V. N. Shanin, L. G. Khanina, P. Y. Grabarnik, M. N. Stamenov, N. V. Ivanova, Nat. Cons. Res. **7(Suppl.1)**, 24-37 (2022). <https://dx.doi.org/10.24189/ncr.2022.013>
10. O. Ovaskainen, S. Skorokhodova, M. Yakovleva, A. Sukhov, A. Kutenkov, N. Kutenkova, A. Shcherbakov, E. Meyke, M. del Mar Delgado, Proc. Nat. Acad. Sci. United States Amer. **110(33)**, 13434-13439 (2013)

11. Z. Tao, H. Wang, Y. Liu, Y. Xu, J. Dai, *Intern. J. Rem. Sens.* **38(11)**, 3236-3252 (2017).
<https://dx.doi.org/10.1080/01431161.2017.1292070>
12. A. A. Minin, A. A. Ananin, Yu. A. Buyvolov, E. G. Larin, P. A. Lebedev, N. V. Polikarpova, I. V. Prokosheva, M. I. Rudenko, I. I. Sapelnikova, V. G. Fedotova, E. A. Shuyskaya, M. V. Yakovleva, O. V. Yantser, *Nat. Cons. Res.* **5(4)**, 89-110 (2020).
<https://dx.doi.org/10.24189/ncr.2020.060>
13. O. E. Korotkova, *Proc. Mord. State Nat. Res.* **28**, 199-207 (2021)
14. J. R. K. Forrest, *Curr. Opin. Insect Sci.* **17**, 49-54 (2016).
<https://doi.org/10.1016/j.cois.2016.07.002>
15. M. E. Karimova, A. I. Damaskin, *Proc. Mord. State Nat. Res.* **28**, 96-101 (2021)
16. A. A. Ananin, *Nat. Cons. Res.* **7(2)**, 66-80 (2022).
<https://dx.doi.org/10.24189/ncr.2022.021>
17. F. Chidawanyika, C. Nyamukondiwa, L. Strathie, K. Fischer, *PLoS ONE* **12(1)**, e0169371 (2017). <https://doi.org/10.1371/journal.pone.0169371>
18. E. Zengin, *Rev. Soc. Entomol. Arg.* **79(1)**, 21-30 (2020).
<https://doi.org/10.25085/rsea.790104>
19. K. Handley, J. Hough-Goldstein, L. M. Hanks, J. G. Millar, V. D'Amico, *Ann. Entomol. Soc. Am.* **108(3)**, 251-262 (2015)
20. S. J. Brooks, A. Self, G. D. Powney, W. D. Pearse, M. Penn, G. L. J. Paterson, *Ecography*. **40**, 1152-1165 (2017). <https://doi.org/10.1111/ecog.02658>
21. A. B. Ruchin, L. V. Egorov, *Redia* **101**, 143-146 (2018)
22. A. B. Ruchin, L. V. Egorov, G. B. Semishin, *Biodiversitas*. **19(4)**, 1352-1365 (2018).
<https://dx.doi.org/10.13057/biodiv/d190423>
23. A. B. Ruchin, L. V. Egorov, A. A. Khapugin, *Ecol. Quest.* **32(1)**, 37-53 (2021).
<http://dx.doi.org/10.12775/EQ.2021.004>
24. A. V. Zemoglyadchuk, A. B. Ruchin, L. V. Egorov, *Entomol. Rev.* **100**, 771-787 (2020).
<https://dx.doi.org/10.1134/S0013873820060068>
25. A. V. Polevoi, *Nat. Cons. Res.* **6(1)**, 5-16 (2021).
<https://dx.doi.org/10.24189/ncr.2021.001>
26. A. B. Ruchin, *Biodiversitas* **22(5)**, 2569-2575 (2021).
<https://dx.doi.org/10.13057/biodiv/d220515>
27. A. Zouaimia, Y. Adjami, R. Zebsa, A. Youcefi, Z. Bensakhri, S. Bensouilah, H. Amari, M.-L. Ouakid, M. Houhamdi, H. Mahdjoub, R. Khelifa, *Nat. Cons. Res.* **7(1)**, 1-9 (2022).
<https://dx.doi.org/10.24189/ncr.2022.003>
28. A. B. Ruchin, M. N. Esin, *Bios. Divers* **29(4)**, 374-379 (2021).
<https://dx.doi.org/10.15421/012147>
29. S. E. Rodríguez-Rodríguez, H. González-Hernández, E. Rodríguez-Leyva, J. R. Lomelí-Flores, M. A. Miranda-Salcedo, *Florida Entomol* **101**, 113-118 (2018)
30. O. Šebesta, I. Gelbič, J. Peško, *Italian J. Zool.* **80**, 125-138 (2013).
<https://dx.doi.org/10.1080/11250003.2012.753119>
31. F. Azza, E. Lucas, D. Gérard, *Agric. Nat. Res.* **54**, 158-164 (2020)
32. A. B. Ruchin, L. V. Egorov, A. A. Khapugin, N. E. Vikhrev, M. N. Esin, *Nat. Cons. Res.* **5(1)**, 87-108 (2020). <https://dx.doi.org/10.24189/ncr.2020.008>
33. E. P. Narchuk, *Proc. Zool. Inst.* **294**, 1-251 (2003)
34. E. Preisser, D. C. Smith, M. D. Lowman, *Selbyana* **19(2)**, 141-146 (1998)

35. M. S. Bogojevic, E. Merdic, N. Turic, Ž. Jeličić, Ž. Zahirovic, I. Vrucina, S. Merdic, *Biologia* **64/4**, 760-767 (2009)
36. L. S. Nekrasova, Y. L. Vigorov, A. Yu. Vigorov, *Rus. J. Ecol.* **47**, 186-193 (2016)
37. K. H. Mali, S. P. Zambare, *Int. J. Life Sciences.* **A13**, 19-23 (2019)
38. H. C. Osório, J. Rocha, R. Roquette, N. M. Guerreiro, L. Zé-Zé, F. Amaro, M. Silva, M. J. Alves, *Int. J. Environ. Res. Public Health* **17(19)**, 7083 (2020)
39. V. Hernández-Ortiz, J. F. Dzul-Cauich, M. Madora, R. Coates, *Neotr. Entom* **51**, 499-513 (2022). <https://doi.org/10.1007/s13744-022-00965-8>
40. N. G. Gornostaev, A. B. Ruchin, M. N. Esin, A. M. Kulikov, *Insects* **13**, 751 (2022). <https://doi.org/10.3390/insects13080751>
41. D. A. Carrero, D. Melo, S. Uribe, K. A. G. Wyckhuys, *J. Pest. Sci.* **86**, 437-447 (2013). <https://doi.org/10.1007/s10340-013-0487-9>
42. I. MacGowan, *Entomol. Tidskr.* **136(4)**, 165-172 (2015)
43. K. Abbes, A. Hafsi, A. Harbi, M. Mars, B. Chermiti, *Phytoparas.* **49**, 49-59 (2021). <https://doi.org/10.1007/s12600-020-00871-y>
44. J. Roháček, *Čas. Slez. Muz. Opava. (A)* **62**, 125-136 (2013)
45. Y. Q. Xi, D. Yang, X. M. Yin, *Zookeys.* **760**, 143-157 (2018). <https://dx.doi.org/10.3897/zookeys.760.22595>
46. N. P. Krivosheina, M. G. Krivosheina, *Nat. Cons. Res.* **4(3)**, 78-92 (2019)
47. A. Soszyńska-Maj, A. J. Woźnica, *Eur. J. Entomol* **113**, 279-294 (2016)
48. R. Bažok, M. Ceranić-Sertić, J. I. Barčić, J. Borošić, A. Kozina, T. Kos, D. Lemić, M. Čačija, *Insects.* **3**, 1001-1027 (2012)
49. J. Sweeney, J. Turgeon, *Canad. Entomol* **126(1)**, 49-59 (1994). <https://dx.doi.org/10.4039/Ent12649-1>
50. M. Bartak, *Silva Gabr.* **2**, 239-258 (1998)
51. D. Martin-Vega, *Baz. Med. Veter. Entomol* **27**, 64-76 (2013)
52. L. Papp, *Acta Zool. Acad. Sci. Hung* **48(1)**, 197-213 (2002)
53. S. Matuszewski, D. Bajerlein, S. Konwerski, K. Szpila, *For. Sci. Intern* **180**, 61-69 (2008). <https://dx.doi.org/10.1016/j.forsciint.2008.06.015>