ISSN 1067-4136, Russian Journal of Ecology, 2011, Vol. 42, No. 6, pp. 480–484. © Pleiades Publishing, Ltd., 2011.
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The Structure of Ungulate Communities

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Received June 1, 2011

Abstract—The study summarizes the results of a long-term research on the factors influencing the structure of ungulate communities in the southern Russian Far East and Middle Urals. The effect of these factors in communities of the southern Far East is largely complicated by interspecific relationships between ungulates. The role of such relationships in the Middle Urals is less apparent, and the territorial distribution of ungulates is largely determined by anthropogenic transformation of habitats.

Keywords: herbiovores, competition, forage plants, community, anthropogenic impact.

DOI: 10.1134/S1067413611060154

Studies of biodiversity that advance beyond simple estimations of its degree usually address community structure, which is often described in terms of the distribution of species according to their abundance (Ghilarov, 2007; Adler, HilleRisLambers, and Levine, 2007; McGill et al, 2007). The attention is usually focused on communities of the same trophic level and, furthermore, on species sharing the same resources and competing for them in case of resource deficiency (Root, 1967; Chesson, 2000).

Ungulate communities are convenient systems for studies in this field (Putman, 1996). Analyzing the distribution of species according to their abundance in any ungulate community, it may appear easy to compile a list of the main factors influencing this distribution. For an ungulate community, these factors include forage, climate, space free from predators and humans, and probably some others. However, when the work on such a list advances from pure theory to practice, problems start to emerge already at the stage of ranking the factors by importance. It is difficult to determining how these factors affect community structure, and prognosis of potential abundance ratios is complicated and requires cumbersome analysis (Clark, 2010).

Interactions within an ungulate community take place against the background of active anthropogenic transformation of habitats and direct impact of hunting on the majority of species, so that every community is subject to the simultaneous influence of internal competition and the above factors. Presumably, competition in ungulate communities will be better manifested at the local level, while factors related to the anthropogenic transformation of habitats, acting similarly in different habitats, will be more apparent at the regional level.

The results presented below were obtained in the study on the effect of different factors on the structure of ungulate communities in ecosystems of the southern Russian Far East and Middle Urals.

MATERIAL AND METHODS

The study is based on the analysis of data on the spatial distribution of ungulates in comparison with data on changes in the relevant factors. The effect of the trophic factors was studied by comparing geobotanical descriptions of forage vegetation in ungulate habitats and the diets of ungulate species (Sheremet'ev and Prokopenko, 2006; Sheremet'ev, 2009), including estimations of plant biomass and species number. The degree of anthropogenic transformation of habitats was estimated from information on land explication in administrative units of Sverdlovsk oblast. The beta-diversity was estimated by calculating the number of contours per unit area in forest vegetation maps (Korytin and Pogodin, 2002; Korytin, Markov, and Pogodin, 2003).

The population density of ungulates in the Middle Urals was estimated from the official data of winter route censuses obtained over the past 30 years. Data on the abundance distribution of ungulates in the Far East were obtained by methods of area and route censuses (Dunishenko, 2000). In addition, extensive materials from the Far East Branch of the All-Russia Research Institute of Game Management and Fur Farming

(Khabarovsk) were used. The abundance of ungulates was expressed in both absolute and relative units.

In the southern Far East, where the number of ungulate species is greater (seven species: the moose, roe deer, sika deer, red deer, wild boar, Siberian musk deer, and long-tailed goral), attention was focused on the dependence of the structure of ungulate communities on trophic factors; in the Middle Urals, where only four ungulate species occur (the moose, roe deer, wild boar, and reindeer), the effect of anthropogenic factors was mainly analyzed.

RESULTS AND DISCUSSION

Analysis of interrelations in the vegetation–ungulates system in the Russian Far East has revealed a number of dependencies of ungulate community structure on the composition, biomass, and other parameters of plant associations.

The abundance of ungulates per amount of shows a positive correlation with species diversity of forage plants in their habitats ($r = 0.47–0.58$, $p = 0.001$). Species with a greater demand for forage, such as the Siberian musk deer and sika deer, prefer habitats with a higher degree of species diversity. According to our calculations, most of ungulate species do not experience food deficiency in their habitats at the current (medium) population density, but they should have suffered from such a deficiency when their population density was at the highest level recorded over past 50 years. Thus, the trophic factor is of undoubted significance for ungulates, at least in terms of their centennial population dynamics (Sheremet'ev and Prokopenko, 2005).

The structure of ungulate communities is determined to different degrees by the structure of forage vegetation (up to $r = 0.95$, $p = 0.001$). The higher the proportion of food resources consumed, the stronger this dependence. Success in interspecific competition depends not only on adaptive advantages of consumers but also on foraging benefits provided to these species by the vegetation of their habitats: the greater the variety of forage plants in the consumer's diet, the higher the abundance of this consumer in a given habitat (Sheremet'ev, 2009).

The ungulate communities of the southern Russian Far East have not been subject to substantial structural changes over the past century: none of the species has been driven to the brink of extinction or undergone large-scale expansion. Nevertheless, there have been considerable changes in the abundance ratio of ungulate species. Over the past decades, a number of areas in the southern Far East have seen a considerable increase in the population density of the sika deer. This species started to disperse mainly over the administrative districts of Primorye, although it has also been reported from southern Khabarovsk krai (Dunishenko, 2000). This coincided with a decrease in the population density of the red deer and roe deer, especially in their common habitats, i.e., there seems to be a certain sequence in the replacement of dominants in ungulate communities. In those communities that chronologically can be considered initial, species do not compete, or at least do not displace their competitors, having neither any substantial foraging benefits nor adaptive advantages. In newly formed communities, some ungulate species are capable of dominating and even displacing other ungulates by using their adaptive advantages to a greater degree than benefits offered by the vegetation. Food deficiency and competition in consumer communities may be indicative of current community replacement or at least of the novelty of guilds.

Competitive relationships in communities develop against the background of strong influence of habitat-transforming factors, the strongest of them probably being anthropogenic. Changes in the species diversity of forage plants resulting from anthropogenic transformations of vegetation lead to changes in the structure of ungulate communities, which can be illustrated by the example of changes in the ranking of ungulate species with respect to the species diversity of their forage plants. Figure 1 shows how timber harvesting in Siberian pine–broadleaf forests and consequent floristic succession have allowed the sika deer to gain considerable advantage over the roe and red deer. Anthropogenic transformation of habitats provides for an increase in the number of plant species in diets of some ungulate species. As a result, these consumers become more successful as competitors; i.e., their abundance increases, while that of other species decreases.

In the Middle Urals, intensification of timber harvesting resulted in an increase in the abundance of moose and a decrease in the abundance of reindeer due to the cutting of sphagnum pine forests, an intermediate habitat of the latter species (Syroechkovskii, 1986; Bol'shakov et al., 2009).

On the eastern macroslope of the Middle Urals and in the adjacent plains, the moose forms five associations differing in population density and type of population dynamics (Pogodin, 1996). Their boundaries show 80% coincidence with those of forest vegetation districts and provinces according to Kolesnikov (1973). Therefore, subzonal features of vegetation determine to some extent both similarity and differences between moose dynamics within these associations. The growth of moose abundance since the late 1940s is related to intensification of timber harvesting ($r = 0.6$, $p < 0.01$) and, therefore, to the consequent increase in the supply of basic winter forage for moose in young tree stands developing in cutover areas. However, the current spatial distribution of moose does not depend on the proportion of young tree stands in the structure of vegetation, which explains only 9% of variance in the average population density of this species in the administrative district. The current population density is considerably lower than the holding capacity of habitats calculated with regard to the food factor, showing that the effect of forage supply on the

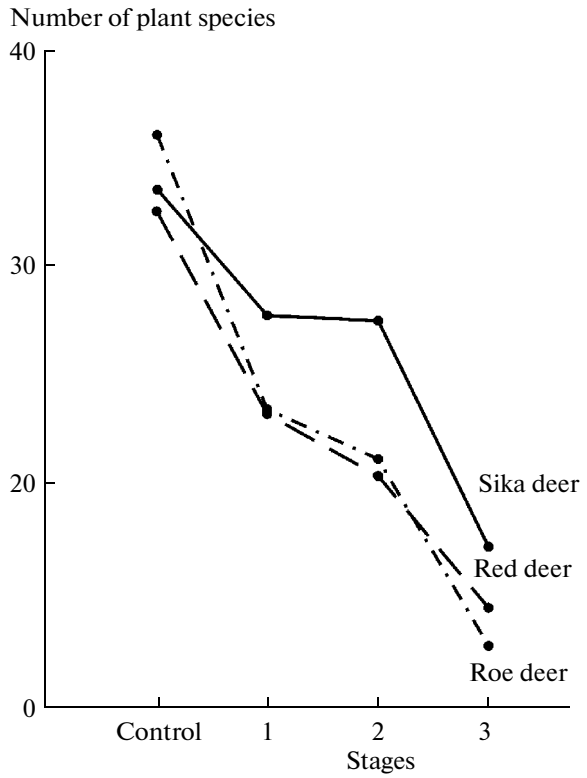

Fig. 1. Changes in the numbers of plant species of moderate forage value in the course of anthropogenic transformation of habitats of tree ungulate species in Siberian pine–broadleaf forests of the southern Russian Far East: control, undisturbed Siberian pine forests; (*1–3*) stages of transformation: (*1*) selective felling areas, (*2*) forests devoid of the main forest-forming species, (*3*) herb–shrub phytocenoses in place of Siberian pine forests.

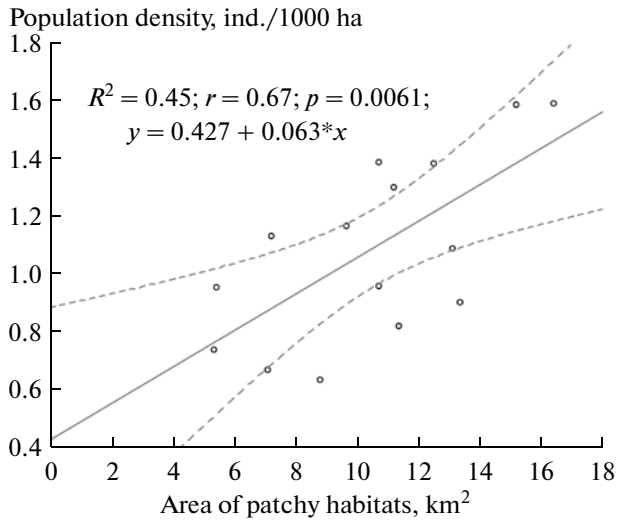

Fig. 2. Dependence of changes in moose population density on the degree of patchiness of its habitats in the northern Sverdlovsk oblast.

spatial distribution of moose is minor (Bol'shakov et al., 2009).

In northern Sverdlovsk oblast, where the level of anthropogenic transformation of habitats is relatively low, the moose responds to the degree of patchiness in the pattern of forest areas (resulting mainly from tree cutting): the more patchy the pattern, the higher the moose population density (Fig. 2). The spatial distribution of moose shows no dependence on the proportion of farmlands, which is relatively low in the region.

In southern Sverdlovsk oblast, where the moose population density in the southern taiga and the level of land transformation are higher, the number of animals per unit area changes in direct proportion to the amount of forests (Fig. 3) and in inverse proportion to the amount of farmlands ($R^2 = 0.64$, $r = -0.8$; $p = 0.000005$), and shows no dependence on mosaic pattern.

Associations of two other ungulate species, the wild boar and roe deer, are subject to even greater influence of anthropogenic transformation of habitats. In northern Sverdlovsk oblast, in the middle taiga subzone, these species live only in areas where farmlands are abundant (Figs. 4, 5) and the patchiness of forests is higher (wild boar: $R^2 = 0.29$, $r = 0.54$, $p = 0.037$; roe deer: $r = 0.55$; $p = 0.035$). In the southern part of the oblast, in the southern taiga and pre-forest–steppe pine–birch forest subzones, population density of these species also largely depends on the proportion of agricultural landscapes (wild boar: $R^2 = 0.45$, $r = 0.67$, $p = 0.0006$; roe deer: $R^2 = 0.52$, $r = 0.72$, $p = 0.00007$).

The population density of roe deer is the highest in areas where the proportion of farmlands exceeds 50%. Roe deer and wild boars actively utilize large forage resources of farmlands. Moose rarely forage in such areas, preferring habitats with a small proportion of fields.

The ungulate communities of the Middle Urals have undergone dramatic changes over the past century. In the late 19th century, they included the reindeer, moose, roe deer, and red deer (Kirikov, 1966; Sabaneev, 1988). These species are listed in order of decreasing population density and range size. Reindeer lived in the northern, middle, and southern taiga and in mountain forests down to the southern limits of the Urals. The roe deer and red deer occupied a limited area. The red deer disappeared from the region by the early 20th century. The range of reindeer became considerably smaller In the second half of the 20th century, simultaneously with its reduction in Europe. Today, reindeer inhabit small isolated foci in sparsely populated mountain areas, in the northern taiga subzone and in the northern part of the middle taiga subzone. Hunting and anthropogenic transformation of habitats are regarded as the main factors responsible for the above processes.

The moose and roe deer, on the contrary, have expanded their ranges during the 20th century and occupied the pre-forest–steppe pine–birch forest subzone and the northern forest–steppe. In the 1970

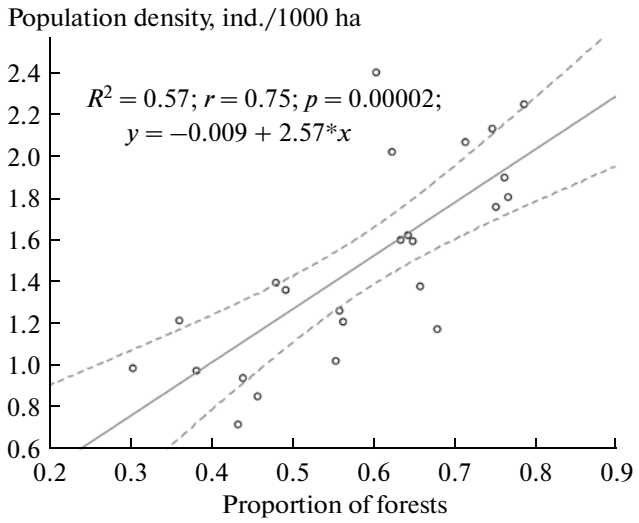

Fig. 3. Dependence of changes in moose population density on the proportion of forested areas in administrative districts of southern Sverdlovsk oblast.

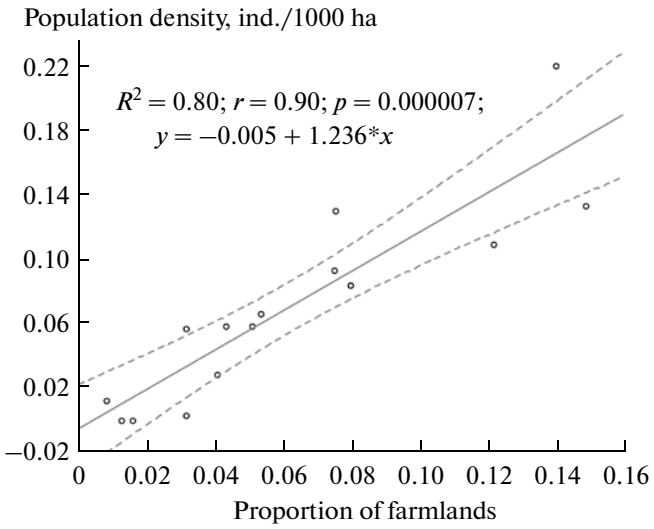

Fig. 4. Dependence of wild boar population density on the proportion of farmlands in northern Sverdlovsk oblast.

and 1980s, the wild boar was deliberately introduced in the Middle Urals. This coincided with the expansion of its range in European Russia. The eastern macroslope of the Middle Urals was partly colonized by the wild boar spontaneously.

The current list of ungulates in the same order of decreasing population density and range size will be as follows: the moose, roe deer, wild boar, and reindeer. Thus, changes in ungulate population density and distribution over the past century can well be explained by either direct extermination, as in the case of red deer, or expansion of anthropogenic landscapes. It should be noted, however, that the latter factor leads not only to an increased patchiness of habitats but also to rearrangements in the structure of pastures that provide more advantages for new dominants.

Such rearrangements, which account for changes in the structure of ungulate communities, can be observed in the course of anthropogenic transformation of vegetation in the southern Russian Far East (Fig. 1). The results of this study provide evidence for a considerable effect of the trophic factor on the abundance and spatial distribution of ungulate species; the influence of the anthropogenic factor is minor, compared to that in the Middle Urals, where ungulate communities have changed over the past 100–150 to the same degree as they did in the Russian Far East in the Early Holocene (Matyushkin, 1972; Ovodov, 1977). None of the ungulate species was exterminated in the Far East during the same period. The boundaries of their also did not change significantly at the regional level. Judging from the average human population density in Primorye, which is only half that in Sverdlovsk oblast, the degree of anthropogenic transformation of habitats in the Far East is apparently also lower than in the Middle Urals.

The abundance ratio of ungulate species in the Far East can be largely explained and, therefore, predicted, on the basis of proportions of forage plants in their habitats. This suggests a certain effect of interspecific competition for food resources, which ultimately results in the formation of monospecific ungulate communities. The effect of extermination as an anthropogenic factor on the structure of ungulate communities is significant only at the level of administrative districts. The effect of anthropogenic changes of vegetation demonstrates the same dynamics as those revealed in studies on the relationship between the abundance ratio of ungulates and the proportions of their forage plants in undisturbed habitats.

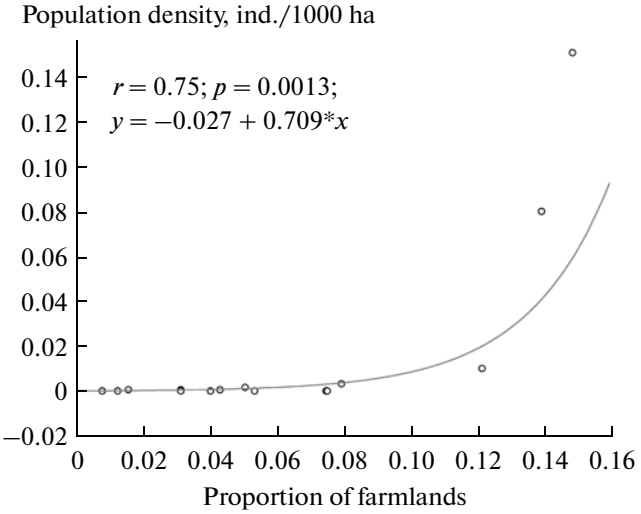

Fig. 5. Dependence of changes in roe deer population density on the proportion of farmlands in northern Sverdlovsk oblast.

ACKNOWLEGMENTS

The authors are grateful to E.A. Pimenova, V.P. Verkholat, and S.V. Prokopenko for their help in collecting the geobotanical material and to N.I. Markov and N.L. Pogodin for their help in collecting and processing the data on ungulate abundance and distribution.

This study was supported by the Far East and Ural branches of the Russian Academy of Sciences (project nos. 06-II-UO-06-010 and 09-S-4-1003) and by the Presidium of the Russian Academy of Sciences (project no. 09-I-OBN-05).

REFERENCES

Adler, P.B., HilleRisLambers, J., and Levine, J.M., A Niche for Neutrality, Ecol. Lett., 2007, vol. 10, no. 2, pp. 95–104.

Bol'shakov, V.N., Korytin, N.S., Markov, N.I., and Pogodin, N.L., Kopytnye (Mammalia, Artiodactyla) na Srednem Urale [Ungulates (Mammalia, Artiodactyla) in the Middle Urals], Yekaterinburg: Ural. Otd. Ross. Akad. Nauk, 2009.

Chesson, P., Mechanisms of Maintenance of Species Diversity, Ann. Rev. Ecol. Syst., 2000, vol. 31, pp. 343–366.

Clark, J.S., Individuals and the Variation Needed for High Species Diversity in Forest Trees, Science, 2010, vol. 327, pp. 1129–1132.

Dunishenko, Yu.M., Lovtsam okhotnich'ei udachi (To Those Who Seek Good Luck in Hunting), Khabarovsk: VNIIOZ, 2000.

Ghilarov, A.M., From Niches to Neutrality in Biological Community, Priroda (Moscow), 2007, no. 11, pp. 29–37.

Kirikov, S.V., Promyslovye zhivotnye, prirodnaya sreda i chelovek (Game Animals, Natural Environment, and Man), Moscow: Nauka, 1966.

Kolesnikov, B.P., Lesorastitel'nye usloviya i tipy lesov Sverdlovskoi oblasti (Site Conditions and Forest Types in Sverdlovsk Oblast), Sverdlovsk: Ural. Nauch. Tsentr Akad. Nauk SSSR, 1973.

Korytin, N.S. and Pogodin, N.L., Spatial Distribution of Moose in Sverdlovsk Oblast and Factors Determining It, Sovremennye problemy prirodopol'zovaniya, okhotovedeniya i zverovodstva: Mat-ly Mezhdun. nauch.-praktich. konf., posvyashchennoi 80-letiyu VNIIOZ (Current Problems in Nature Resource Exploitation, Game Management, and Fur Farming: Proc. Int. Sci.–Pract. Conf. Dedicated to the 80th Anniversary of the All-Russia Research Institute of Hunting and Fur Farming), Kirov, 2002, pp. 276–278.

Korytin, N.S., Markov, N.I., and Pogodin, N.L., Land Patchiness As a Factor Determining the Level of Ungulate Population Density, Dinamika populyatsii okhotnich'ikh zhivotnykh Severnoi Evropy: Mat-ly III mezhdun. simpoziuma (Dynamics of Game Animal Populations in Northern Europe: Proc. III Int. Symp.), Petrozavodsk, 2003, pp. 119–122.

Matyushkin, E.N., Mixed Pattern of Theriofauna in the Ussuri Region: General Features, Historical Sources, and Current Manifestations in Communities of the Middle Sikhote-Alin, in Issledovaniya po faune Sovetskogo Soyuza (mlekopitayushchie) (Studies on the Fauna of the Soviet Union: Mammals), Moscow: Mosk. Gos. Univ., 1972, pp. 86–144.

McGill, B.J., Etienne, R.S., Gray, J.S., et al., Species Abundance Distributions: Moving beyond Single Prediction Theories to Integration within an Ecological Framework, Ecol. Lett., 2007, vol. 10, no. 10, pp. 995–1015.

Ovodov, N.D., The Late Anthropogene Fauna of Mammals (Mammalia) in the Southern Ussuri Region, in Fauna i sistematika pozvonochnykh Sibiri (The Fauna and Systematics of Vertebrates in Siberia), Novosibirsk: Nauka, 1977, pp. 157–177.

Pogodin, N.L., Estimation of Similarity in Moose Population Dynamics between Different Regions of Sverdlovsk Oblast, in Problemy obshchei i prikladnoi ekologii (Problems in General and Applied Ecology), Yekaterinburg, 1996, pp. 173–183.

Putman, R., Competition and Resources Partitioning in Temperate Ungulate Assemblies, London: Chapman & Hall, 1996.

Root, R.B., The Niche Exploitation Pattern of the Blue-Gray Gnatcatcher, Ecol. Monogr., 1967, vol. 37, pp. 317–350.

Sabaneev, L.P., Okhotnich'i zveri (Game Animals), Kalganov, E.A., Ed., Moscow: Fizkul'tura i Sport, 1988.

Sheremet'ev, I.S., The Effect of Quantitative Variables of Forage Vegetation on the Structure of Ruminant Guilds, Russ. J. Ecol., Ekologiya, 2009, no. 5, pp. 336–341.

Sheremet'ev, I.S. and Prokopenko, S.V., General Analysis of Forest Vegetation in the South of the Far East with Regard to the Feeding of Wild Ruminants (Artiodactyla, Ruminantia), Russ. J. Ecol., 2006, no. 4, pp. 217–224.

Syroechkovskii, E.E., Severnyi olen' (The Reindeer), Moscow: Agropromizdat, 1986.