STRUCTURE OF MOOSE (*ALCES ALCES*) POPULATIONS IN RUSSIA WITH SPECIAL REFERENCE TO COMMUNICATION DISTANCES

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ABSTRACT: The structure of moose populations was studied in the southern subzone of taiga and mixed forests. Moose were distributed irregularly in small groups. Some migrations were recorded. The distance between moose in compact groups (5–9.3 m) and the distance between groups were compared to orientation vectors *a–k*, representing one of the parameters of the inner activity rhythms. The distances and the vectors correspond to the definition of the critical levels of the development of natural systems. The spatial pattern of moose distribution was revealed and a canonic distribution model developed.

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Key words: activity rhythms, behavior, distances between moose, ecology, hierarchical structures, natural systems, population structure, social groupings

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The spatial structures of moose populations are diverse and their most important properties should be determined. This study examines spatial structures of a moose population and shows regular utilization of habitats by dispersing moose. A model is suggested that may be used to search moose habitats, estimate moose population size, and predict the distribution of moose without a complete census.

STUDY AREA

The behavior and ecology of moose (*Alces alces alces*) was studied in the Yaroslavl, Kostroma, and Moscow regions of Russia. Vegetation is at the southern limits of taiga and boreal mixed forests, including birch forests, aspen forests, willow thickets, and also spruce and mixed forests. Moose density ranged from 0.3 to 2.2 moose per km^2 in the Yaroslavl and Kostroma Regions (300 km^2). Moose density in the Kostroma Region was 0.2–0.9 moose per km^2. In Sikhote–Alin forests, moose (*Alces alces cameloides* Milne–Edwards 1867) density was only 0.01–0.2 moose per km^2. Localized high density concentrations were near salt licks.

METHODS

Moose were observed throughout the year and monitored day and night. A night vision device was used when it was dark. We recorded the distribution of tracks, bedding sites, locations of mating areas, camps, and fecal pellet groups.

RESULTS

At Yaroslavl, moose tracks are found throughout the entire area, but moose concentrate at certain sites in the forest. A total of 5 main groups occupy an area of 2–10 km^2 in the 300 km^2 forest (Naumov 1967). Each group consisted of 1 8–year–old male, 2 1–4–year–old males, 3 females, and 2 calves. All members of groups were observed in close proximity day and night in winter. Yearlings and 2–3–year–old moose migrate from one forest to another in spring and summer. Cows concentrated at the sites of future calving in spring. Approximately 67–85% of shrub layer stems showed evidence of browsing.

The distance between individuals in compact moose groups was 5 m (n = 24, range = 3–12 m) when other groups were present and 9.3 m (n = 8) when other groups were absent in December and January. In meadows and shrub vegetation, the distance between compact groups was 25.7 m (n = 80, range = 10–50 m). The distance between compact groups was 150 – 400 m in winter, with a maximum distance of 1600 m ($\overline{X}$ = 700 m, n = 7). Compact groups are close enough to quickly find one another. I refer to this distance as the distance of sensory detection (*M*). In spring and summer the distance between moose which are members of a group is similar to the distance between groups (Fig. 1).

Communication distances (*A, K*) were compared to the orientation vectors, whose system (*a,R* – behavioral system) was previously known (Zaitsev 1991) from work with musk deer (*Moschus moschiferus* L.). The *a*–vectors represent orientation to close landmarks such as high forage densities or sites where obstacles are overcome. For moose, *a*–vectors when snow is present are equal to 11.3 ± 0.81 m (n = 37, C.V. = 44%) and in summer *a*–vectors are 8 ± 0.62 m (n = 37, C.V. = 17%). The difference (0.01 > P > 0.1) coincides with changes in the distance between groups in winter and summer. The *v*–vectors are directed to landmarks at a medium distance such as groups of camps (summer and winter) or bedding sites. The *v*–vectors in summer are 51.7 m (n = 10, range = 29–87 m). The *k*–vectors represent orientation to farther landmarks such as relief features and neighboring plots that are 200 – 1,500 m away.

All the vectors communicate by continuous passages. Since *a, k* is a behavioral system, changes in the direction of movement are also observed in the stimuli causing orientation in movement. These changes are reflected in the inner activity rhythm as adapted to the main structural elements of the environment.

The rhythm of movement is set up by an alternation of distances between trees, accumulation of food, and the relief structure. Communication distances increase 5 – 15 times from distances between trees to relief structure. Orientation vectors increase 5 – 12 times, which is characteristic of the critical levels of development of a natural system (Zhirmunsky and Kuzmin 1990). The mean values of *X* of the vectors and communication distances mark the waves of a general adaptive rhythm of alternation

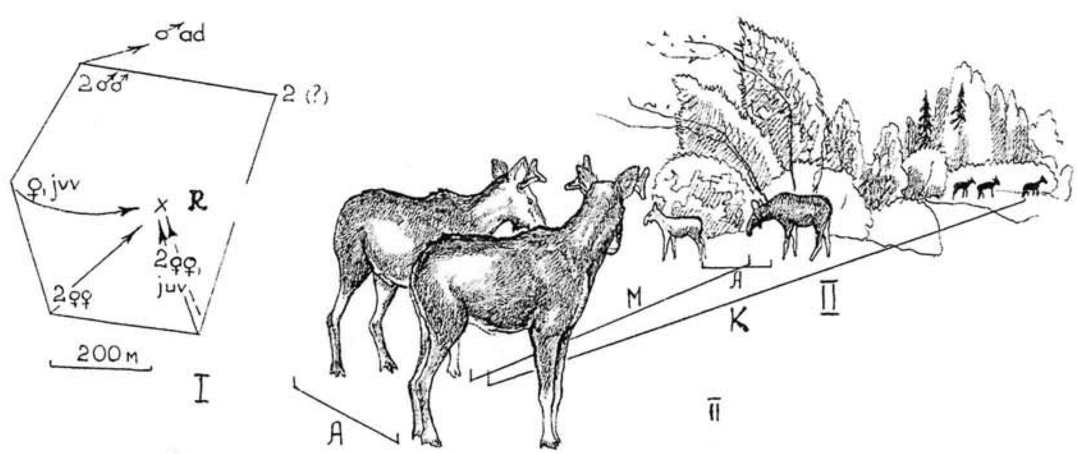

Fig. 1. Disposition of moose in relation to one another and communication distances *A, M, K* (II). *A* –individual distance; *M* – distance of direct sensory contacts; *K* – distance of communication corresponding to vector *k* of orientation; *R* – assembly site.

of various behaviors and orientations (Fig. 2), which are the cells of quantum space. The size of cells is determined by the formula: $S_r = Gx|v|^2$, where v is an orientation vector, x is an asymmetry coefficient, and G_a = 28–271 m^2, G_m = 1.6x10^{-4} – 2x10^{-3} km^2, and G_k = 7.1x10^{-3} – 1.54 km^2.

The G_k cells are commensurate with the size of the home range that moose occupy under different conditions (Heptner and Nasimovitch 1967, Filonov 1983). The vector k of the G_k cell being of sufficient length, the G_k cells are comparable to the size of the "yards" (Knorre 1959, Yazan 1961) that must be occupied by a group of moose.

The distribution of individuals and groupings followed a specific pattern. Moose occupied constant or temporary sites around the central part of the grouping (Fig. 3). Around an individual or a group situated in the center of an area at the distances of m– and k–vectors, there were 4 – 6 other individuals or groups at a density of 0.8–1.2 moose per km^2. Adult males occupied the central place of the grouping or remained at some distance from the other members of

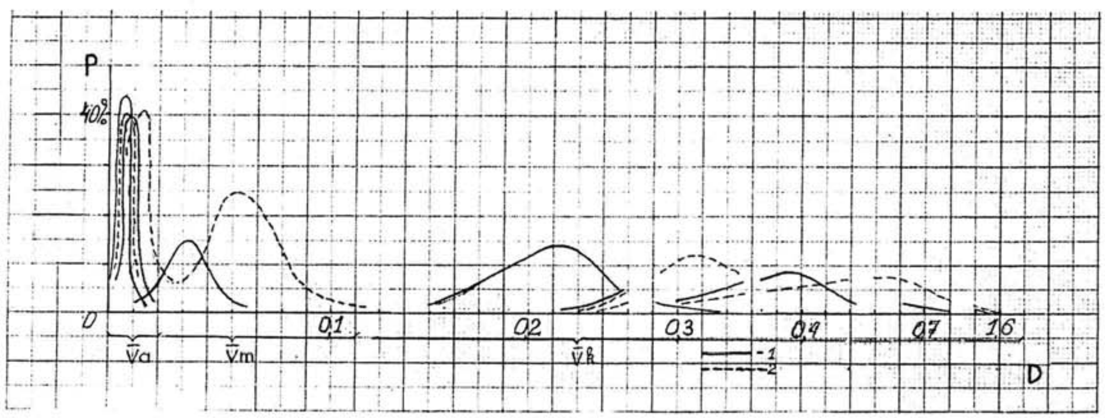

Fig. 2. Statistical waves of distances and veetors of moose orientation. P – percentage of observations of distances; D – distance (km). V – mean values; 1 – distance; 2 – orientation vector.

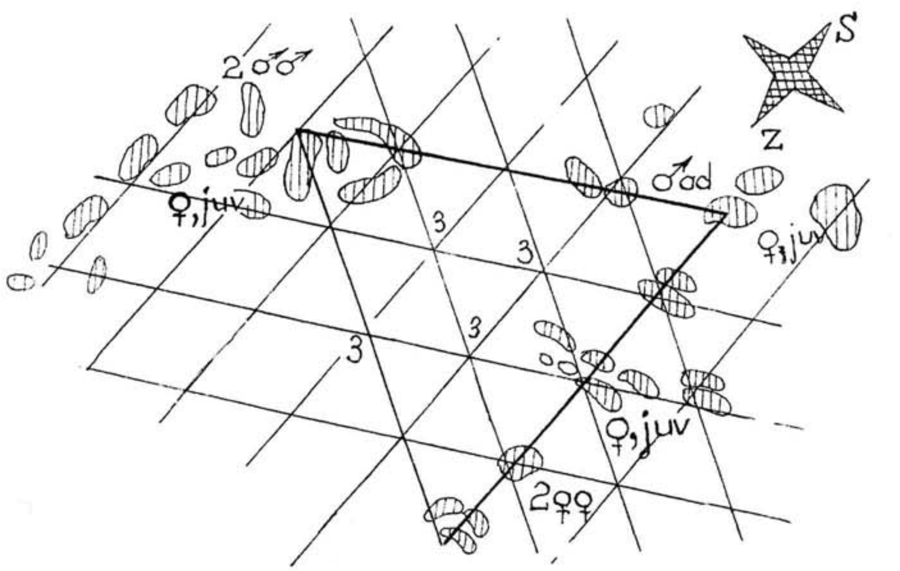

Fig. 3. Distribution of bedding and group sites in the home range of a group.

the group. The angle between the direction to closest neighbors varied from 32 – 100° (X = 63°). This population structure reflects the intention of the animals to resume contacts with one another. The distribution of the bedding sites, camps, and moose is characterized by triangles with home ranges that are fairly homogeneous in structure. The geometrical properties are retained at different population densities.

A canonic model of the structure of a moose population was developed (Fig. 4) and tested for various densities of moose populations. Choosing the respective direction, we invariably found either moose themselves or a concentration of their tracks or signs of their activity in appropriate home ranges at a distance of *m–* and *k–*vectors. Deviations from the model's predictions increase when the moose have no contacts among themselves for a long time.

CONCLUSION

The heterogeneity of the distribution of moose is determined by the mosaic dispersal of critical factors, representing a population structure property. Small groupings are formed by animals that have frequent contacts with one another in a small area (2–10 km²). The small area is used constantly with respect to the succession of forest coenoses.

The spatial structure of the population, distances between the individuals, and the system of orientation vectors have a single basis in behavior (activity rhythm) adapted to some critical features of the environment, coenosis structure, relief, and social properties. The elucidation of the hierarchical discrete structures in the utilization of space is of primary importance for further structuring of space. A patterned use of habitat occurs due to the geometric pattern

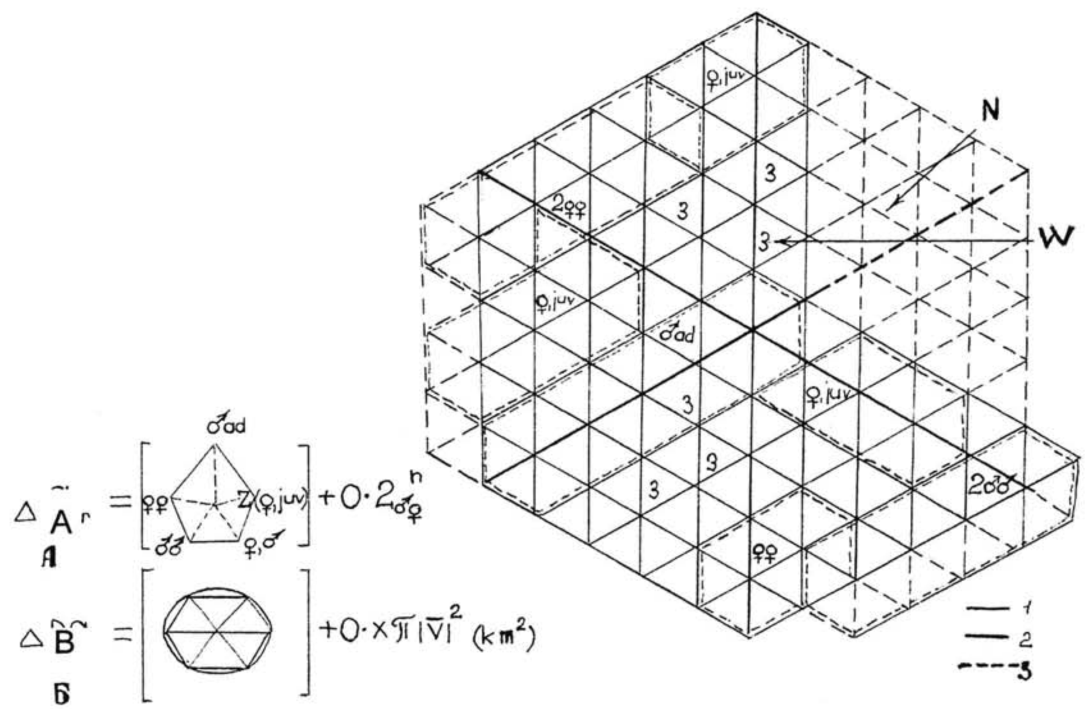

Fig. 4. Spatial organization of a grouping in the web of vectors and communication distances. 1 – vector k_{max}. 2 – vector k_{min}. 3 – cells occupied by moose ranges. A and B – equations of community organization: A – an independent breeding grouping; B – a static organization of the group (spatial structure of the cell). N – unsuitable habitats. W – winter habitats.

in which the activity rhythm is manifested.

Asymmetry features of the distribution of moose over the brief period of time in the course of movement result in symmetrical structures in the distribution of tracks, and, on the whole, to a fairly regular utilization of the habitats. It is possible to use the model to search moose habitats, estimate moose population size, and predict the distribution of moose without a complete census.

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