

The main behavioural changes in the herbivorous game animals in managed forests

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The purpose of this study was to determine the main changes in the behaviour of herbivorous game, and to reveal the effect of these changes on the animal—plant interaction in managed forests. The behaviour of animals was tested by direct observations and indirectly by observations of changes in the animal movement dynamics. Forest and game management changes the social behaviour, which includes all types of animal interactions. Eventually the changes become needs. The allowance for a state of animal behavioural types (such as stability or changes of ones) could help foresee possible deviations and the impact of herbivores on the forest vegetation as well as in consideration of the animal philopatry, directions of movement in the habitats.

Key words: Herbivores, behavioural types, need, managed forests

Introduction

The herbivorous game such as ungulates, hares are an important component of forest ecosystems. The natural interaction between the animals and forest vegetation has changed due to the constant and changeable factors that associate with forest use (such as harvesting, forest fragmentation, management of animal populations, hunting, etc.). The economic significance of the herbivorous game animals rather depends on the specific character of their feeding (browsing and bark stripping). The herbivorous animals influence forest development and diminish the success of forest regeneration. They also cause changes in the forest composition and diversity. The special digestive system, morphological—physiological and behavioural features of the herbivorous game animals determine their impact on the available woody vegetation, layer of small shrubs in the animal feeding space, notably within the later autumn—early spring period. This period will be under consideration. For the herbivores—forest vegetation interaction such features are important: plant age, height, morphology, qualitative composition, plant capability to defend itself (self—preservation), and even the reciprocal reactions of animals (choice—avoidance reactions). The foraging strategy of animals is inseparably linked with ecological niches. A change in the niche parameters has an influence on animal relationships, animal—plant interaction, state of forest key species

(Belova, 1997). Then, the changes in niche parameters do not relate only to seasonal changes in nutrient balance but also to changes of animal behaviour (Petrauk, 1991). The importance of the studies on animal behaviour is attached to management of animal populations (Hofmann, 1980; Lovari et al., 1988; Klopfer and Plemics, 1988; etc.). It is necessary to make allowance for the behavioural motivation (Yueron, 1992) according to an individual variation in the animal behaviour.

The purpose of this study is to determine the main changes of the behaviour of herbivorous game animals, and reveal the importance of these changes in the interactions between the animals and forest plants.

Materials and methods

In accordance with the main purpose of the study of behavioural changes in the herbivorous game animals, such as ungulates and hares, and due to emphasizing of the animal—plants interaction in the managed forests, the belt transect route method was used. The route unit was 4x100 m. All distinguishable signs of animal location were registered. The index of habitat use was calculated: $I_i = \sum N_x / \sum nL / G$, where N_x is the frequency of finding of animal location signs, nL is the number of route unit m, and G is the coefficient of an aggregation (i.e. a unit of the ratio of single to group signs of the animal location such as pellets, tracks, etc.) (Belova, 1990). In addition, the individual tracking meth-

od was used in snow ($n=23$ observations). The feeding relations were studied by the sample plot method. The number of sample plots (5×10 m, $n=632$, and 10×10 m, $n=140$ of ones) was 2 per route unit. Control plots were 1 per route unit. All signs of feeding including the stand characteristics, injury and intact plant species, their features, use pattern — browsing or bark stripping etc., use of plant part, number and distribution of animal pellets were registered. Method of the direct observation and registration of changes in the animal movement dynamics was applied for testing the behaviour of hares and ungulates. The changes in the main behavioural types were analysed on the basis of the data collected on the route as well of the direct observations. The direct observation grounded on the ethogram method. Then ecological features of animals and seasonal changes in them were taken into account. The total duration of the direct observations was 294 h of showings and also 195 h of observations on ungulates separately. The influence of disturbances was also tested by stimulating method (approaching, shooting, etc.). The range of the disturbance included an absence of the disturbance then source of the disturbance is outside of the sensual area, and different kind of the disturbances such as the pursuing, direct frightening, the disturbance during the animal feeding. The total length of the route was 181 km. The total area of six study areas was 11,961 hectares, including 4,047 hectares of deciduous stands, 5,979 hectares of mixed spruce-deciduous stands, 1,688 hectares of pine-spruce stands, and 1,357 hectares of pure pine ones.

Results

Within the later autumn—early spring period the game animals often find themselves in an unusual situation in the managed forests. Disturbances are stronger because of less favourable feeding conditions, such as scarcity and less accessibility of fodder, predominated unfavourable weather conditions (snow cover, changeable air temperatures, inclemency of weather, etc.), and also because of the direct pursuit during the hunting season, logging and other forest use. In the mentioned period the divergence from the norms of behavioural reactions of the ungulates (elk, red deer and roe deer) and hare (European hare) has displayed according to the ratio of the demands. In the usual situation, the hierarchy of behavioural types is such: defensive, feeding, social, sexual, parental, and comfort ones. Then an animal primarily notices a danger, slightly later on — search-

es food, and also groups. The species—specific range of the behavioural reactions depends on the incentive motivation to act and to revert to the state of the equilibrium. In the tested period, the main usual motivation of the animal behaviour is the hunger as the essential key—drive of behaviour. Both behavioural types feeding and defense become of the same importance. These behavioural types are directly linked with the social behaviour including the ranging behaviour too. The social behaviour is very important for the animal—plant interactions, and determined the use of favourable features of the habitats. In accordance with social behaviour Lithuanian herbivorous animals, such as deer *Cervidae* and hares *Leporidae* are satisfactorily social ones, and sometimes get together in the groups. For example, due to continuous anthropogenic changes in the feeding conditions and shelter in the mentioned period, the appropriate irregular random distribution of the hares become clumped random and clumped (when the animals form aggregations in discrete clumps). These temporary aggregations result from clumped distribution of habitat resources and from tendencies of the animals to form small temporary groups in the most favourable places. The average size of a group is 4-8 individuals per one. The groups are not determined by demographic parameters and age limitation. The variance of the index of habitat use on average is $\sigma^2=8.82$ and $V=89.7\%$. It implies random clumped distribution of animals (in our case the distribution is clumped when variance σ^2 exceeds the mean value of index I_i habitat use and the criterion of ratio $\sigma^2/I_i \geq 1$). On the woodland the animals get together in certain habitats of the mixed stands, namely in the *Vaccinio-myrttillosa*, *Oxalido—myrttillosa*, *Vacciniosa*, *Myrttillosa*, *Oxalidososa*, *Hepatico-oxalidososa*, *Carico—mixtoherbosa*, *Urticososa* forest sites. There is index $I_i = 5.36 \pm 0.33$, $G=0.54$ on average, mean square deviation $\sigma = 4.56$, variance $\sigma^2=20.77$, and criterion of clumping $\sigma^2/I_i = 3.88 > 1$ which shows clumped distribution, $p=0.042$. Animals gathered also in the *Mixtoherbosa*, *Carico—mixtoherbosa* forest sites in the deciduous with spruce stands where $I_i = 4.18 \pm 0.55$, $G=0.53$ on average, $\sigma = 4.91$, $\sigma^2=24.13$, $\sigma^2/I_i = 3.36 > 1$. It shows clumped random distribution. The deer (*Cervidae*) also get together in the places of favourable feeding especially in the winter-early spring period. The animal behaviour is synchronized within the aggregations. Within the hare groups the individuals orient themselves towards the source of disturbance (a case of man's approach, the frequency of the orientation reaction is on average $f=5$ of females and $f=3$ of males, the duration is 0.13 min and 0.03 min, respec-

tively) from the distance of 100 ± 8 m. The animals allow a source of disturbance to approach up to 30.0 ± 6.3 m (lim 2.0 ± 62.5) up to the beginning of the hunting season and 619 ± 1.32 m (lim $33.7-90.3$ m) during the hunting season. The leaders run around the group. Then the hares run together at the distance of 300 ± 140.5 m from the mentioned kind of disturbance. The stops ($f=4-9$) and movements of the jumps ($L=1.0-1.3$ m) are characteristic. The animals continue their feeding when the disturbance source turns aside (on average 0.5 ± 0.1 h after the moment of disturbance). In such groups of hares, feeding is facilitated because of reducing the time required for being on the look-out for danger. However, this is characteristic team behaviour of hares, which has been caused by human interference. In the deer groups the individuals as well as hares repeat the actions that are begun by individuals—leaders. These patterns of the animal distribution and main behavioural features have revealed when a disturbance is scant and fragmentary. The essential changes in the behavioural incentives depending on the character of the main disturbances are shown in Figure 1. In our case, the display of a certain range of the

animal behavioural incentives is shown depending on the disturbance pattern from direct pursuing to sudden encounter with a source of disturbance within the animal feeding. Because of unusual and unexpected situations, and also an unfavourable foraging in the above-mentioned period, the usual range of behaviour has disordered. The inadequate behaviour predominates depending on the animal species (such as moose, red deer, roe deer, European hare), age (such as adults and youngsters), sex (male and female), and status of hierarchy. When the essential motivation such as hunger is not satisfied, the animals find themselves in a conflict (Belova, 1989, 1995b). Because of pursuit or other intrusions in the animal feeding space the efficiency of animal feeding diminishes by the rising need to protect itself. The animals are compelled to step aside. The characteristic feature of the deer is fast and sudden retreat depending on the condition of the habitat (woodedness, relief, weather, etc.). The elk behaviour is more like passive defensive—feeding behaviour. This behaviour reveals itself by more intensive feeding, and furthermore by stronger impact on the forest plants. The red deer be-

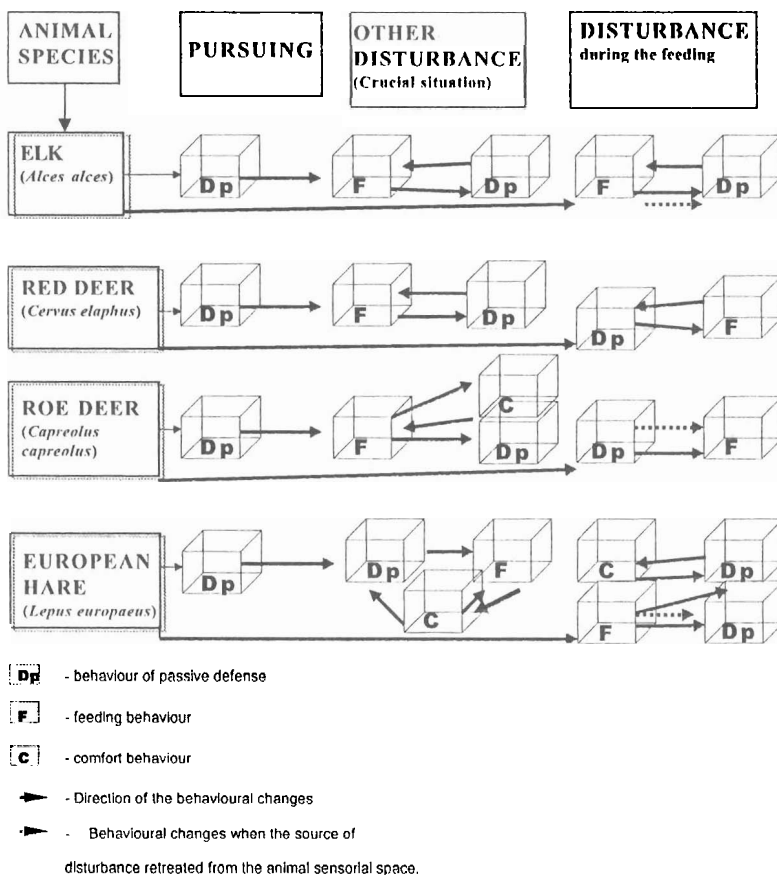


Figure 1. The scheme of changes in the behavioural incentives depending on the character of the disturbance

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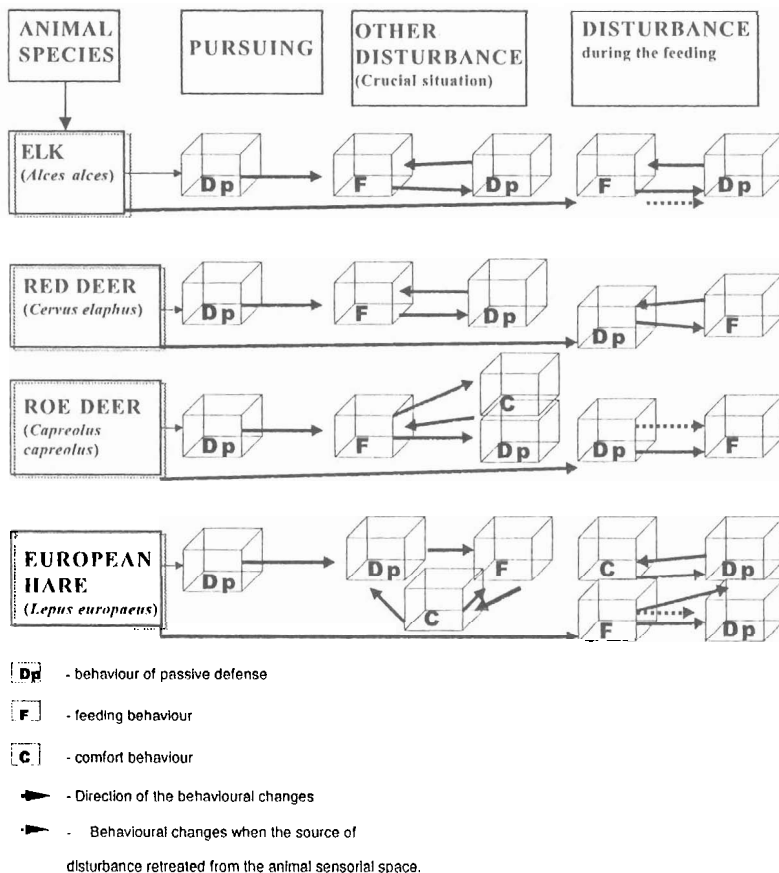


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haviour gives up its place to the feeding behaviour. In crucial situations the feeding usually predominates or the inadequate behaviour is displayed (such as the range of behavioural forms “orientation — feeding — retreat — feeding — comfort reactions — feeding”). The defensive behaviour of the young deer is less displayed while the feeding behaviour predominates, especially in the places of supplemental winter-feeding and near cuttings. Disturbances cause the inadequate behaviour (or the behaviour of discontinued actions) of the hares as well the ambivalent — displacement behaviour that accompanies a crucial situation. Predominated needs are there of the defensive behaviour, feeding behaviour and comfort behaviour. In such situations an animal feeds, cleans itself, runs, cleans itself again (Belova, 1989, 1990). However, the impact on plants is mostly like scattered browsing of plants within the lower layer of the herb and shrubs up to 0.4 m. In the case of the roe deer, red deer and elk, the increasing impact on plants is like the stronger browsing and bark stripping. The disturbed deer strongly strip off the bark of the preferable tree species within the following feeding (meanwhile the ash use is up to 75-100%) directly near the feeding place (5-50 m on average). The usual behavioural actions precede mentioned behaviour, such as orientation (10 seconds), retreat (6 seconds), feeding (30 seconds), and discontinued reactions such as *retreat—feeding—orientation*, when the deer had retreated hastily from the sensorial space of the disturbance source (e.g. incentives like forestry machinery, people, frightening, pursuing). Because of the animal concentration in the places of the favourable living conditions as well as of certain philopatry (however, in the situation of the lack of the same places), the animals have satisfied themselves with secondary food. Within the retreat they especially strip off the bark of ash *Fraxinus excelsior* L., oak *Quercus* L., spruce *Picea* L. or browse shoots of the preferable tree and shrub species such as ash *Fraxinus excelsior* L., oak *Quercus* L., aspen *Populus tremula* L., willows *Salix* L., swallow *Salix caprea* L., peg wood *Euonymus europaeus* L., Norway spruce *Picea abies* L. Karsten and others. The young animals repeat the actions of adults (orientation, repeated actions of the leaders and older animals, also could be separate trying to take initiative for leader's function), and all animals repeat the actions of their leaders and innovators by the imitation. These animals begin to test new food (in this case mistletoe *Viscum album* L. for the deer and special pellets for the hares). They also begin to feed first of a group. An increase in plant use is determined too (Belova, 1988, 1995 a).

Discussion and conclusions

The changes in animal behavioural reactions and norms of these are the adaptation and the sign of species flexibility that depend on the changes in the feeding conditions and habitat features. All behavioural types are important for the animal—forest vegetation interaction. The feeding behaviour, social behaviour including the ranging behaviour, and as well as comfort behaviour are most closely connected with mentioned interaction and revealed themselves all year long. The social behaviour determines the animal interrelations, contacts, distribution and competition for the habitat resources as well population indices. Thus, the territoriality is the factor which maintains the balance between the animal and its environment. The herbivorous animals can change feeding character depending on the accessible fodder composition (Andersen, 1991). The characteristic feature of all herbivores is the behaviour that optimizes the feeding process. First, animals use more thin shoots and more nutritious parts of plants that diminish the use of worthless stuff. Second, the quantity of nutrients is less in longer shoots. This process was emphasized in our studies of the herbivore-plant interaction as well (Belova, 1995b). Thus, the extent of the use of the mentioned parts of a plant is caused by the interaction between the herbivores and plants. The deer and elk use the shoots of woody plants more fast than the bark or herb. The herbivores usually waste time away up to 60-70% of day—time for their foraging depending on food abundance, quality, accessibility and habitat conditions. For instance, the deer on average feed 5-8 times per day (7-10 h) and, moreover, deer ruminate about 5 h (Hofmann, 1984). However, through the fodder shortage the feeding process is lasting, and the animals move more. We could see some ecological rule. That is the length of moving per day negatively related with the forage accessibility and abundance. Meanwhile, the animals lose more energy. This situation is characteristic in winter. At the same time the need of energy increases (Fennessy et al., 1981; Belova, 1989, 1995a,b). Thus the animals can adapt themselves to these natural circumstances. However, the human economic activity in forests changes the usual equilibrium of the forest ecosystems and determines the stronger and changeable impact by herbivores on the forest vegetation. In the usual situation no changes occur in the range of behavioural types. Meanwhile, the inadequate behaviour is displayed in the unusual situation, especially during the specific winter period when the feeding importance becomes the same as the shelter one.

The feeding shortage is accompanied by exterior disturbances and stimulates the grouping effect in the places of more favourable feeding. As to feeding behaviour, the changes in the behavioural reaction norms (i.e. greatest exceeding of the mean animal behavioural action) cause changes in the forage balance. Then the feeding on any secondary fodder becomes usual. For example, birch was not the main fodder of the European hare diet, however, currently it became usual fodder and makes up to 35% of hare diet (Belova, 1989, 1990). The same changes are the tendency of changes in the species behavioural reaction norm. The changes in behavioural reaction norms are accompanied by intrinsic physiological changes as well hung down to the progeny by the imitation, learning and traditions. Eventually the changes become a need. Then the state of the behavioural reaction norm stability could allow us to foresee the possible changes in the herbivore impact on the forest plants taking into consideration animal philopatry, directions of the moving within habitats.

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ОСНОВНЫЕ ПОВЕДЕНЧЕСКИЕ ИЗМЕНЕНИЯ РАСТИТЕЛЬНОЯДНЫХ ОХОТНИЧЬИХ ЖИВОТНЫХ В ХОЗЯЙСТВЕННЫХ ЛЕСАХ

О. Белова

Резюме

Целью настоящей работы было определение основных изменений типов поведения растительноядных животных и выявление последствий этих изменений для взаимодействия животных и растений в хозяйственных лесах. Поведение животных изучалось методом непосредственных наблюдений и косвенно, путем регистрации передвижений животных маршрутным методом. Лесное и охотничье хозяйство изменяют социальное поведение, охватывающее все типы взаимоотношений животных. Постепенно изменения принимают характер потребностей. Принятие во внимание состояния основных типов поведения (их стабильности или изменения) позволяет прогнозировать возможные отклонения поведения и влияния животных на лесную растительность, также учитывая филопатрию животных, направления движения в местообитаниях.

Ключевые слова: растительноядные, типы поведения, потребность, хозяйственные леса.