Vestnik Zoologii, **53**(3): 255–262, 2019
DOI 10.2478/vzoo-2019-0025

UDC 599.6/.73(502.72:262.54)

FORMATION OF INTER-SPECIES LINKS IN UNGULATES IN THE AZOV-SYVASH NATIONAL NATURE PARK

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Formation of Inter-Species Links in Ungulates in the Azov-Sivash National Nature Park. Smagol, V. M., Babich, O. G., Kaminetskyi, V. K., Yarysh, V. L., Smagol, V. O. — The succession of ungulate fauna was studied under conditions of artificially high density and limited residential area on the Biryuchy Island of the Azov-Sivash National Nature Park. Forming of inter-specific relationships between populations of the moufflon, red-deer and fallow-deer were revealed. The social hierarchy of the mentioned species, which are at the same trophic level, is determined. For the population of each species the factors influencing the dynamics of its number are given. Competition of species in steppe habitat is based solely on trophic relationships because the protective properties of the land are minimized. The forage base creates equal conditions for different species, since there is no woody vegetation in the steppe, which makes the large size of the red deer not important for the food obtaining. Concerning the fallow-deer, there is activation in reproductive potential, which is the part of the strategy in competition for resources and indicates its wider ecological lability in comparison with the red-deer. Meanwhile, a high level of adaptation to the conditions of the open steppe is noted in the moufflon, which (together with high reproductive capacity) rationally uses pasture potentials while the fallow-deer and red-deer have a certain level of stenophagy.
Key words: red-deer, fallow-deer, moufflon, competition, dynamics, trophic, fertility.

Introduction

Azov-Syvash National Nature Park (NNP) is situated in the southern-eastern part of Kherson Region within Novotroitske and Henichesk administrative districts. The Biryuchyi Ostriv Spit holds 7273 ha or 86 % of dry land in NPP. The spit is almost everywhere surrounded by water area of the Sea of Azov (at south) and Utljuk firth (at north), and is connected with mainland only by a narrow strait of the Fedotova Spit (Project …, 1995). Length of the peninsula, together with a part of the Fedotova Spit, is 28.6 km, and the maximum width is 5 km. At the northern-eastern border of the peninsula, where its width reaches 200 m approximately, a fence

of 2 m in height is installed, which prevents animals from leaving the protected area and creates semi-free conditions for their maintenance (An instruction …, 2002). Traditionally, territory of the Biryuchyi Ostriv Spit is used for rearing of ungulate species intended for hunting, whose density in the middle of the 2000s reached extremely high levels: over 500 animals per 1 thousand hectares (Domnich, Nesterov, 2005; Kaminetskyi et al., 2011). Under these circumstances, it is logical that competitive relations arise between populations of the same trophic level, which under conditions of artificial restriction of area become extremely sharp.

Material and methods

Quantity dynamics of ungulates on the territory of the Biryuchyi Ostriv Spit has been analyzed since 1928. For this purpose, archive data and regulatory information related to the Azov-Syvash NPP were analyzed; results of own previous researches were taken into consideration (Babich, Kaminetskyi, 2008; Kaminetskyi et al., 2011); during several years the authors directly participated in planned counts of animals (Popovchuk, Kaminetsky, 2008; Smagol et al., 2009).

In the course of the research we investigated the following: changes in number of the red-deer (*Cervus elaphus* Linnaeus, 1758), fallow-deer (*Dama dama* Linnaeus, 1758) and mouflon (*Ovis musimon* Linnaeus, 1758), influence of anthropogenic factors, internal evolutionary mechanisms and inter-species ecological links on their groups. For this purpose, common methodological concepts were applied (Dažo, 1975; Shilov, 1998). Thus, based on investigation of competition between ecologically similar species under conditions of artificially increased density a dynamics of their social hierarchy, with defining dominant and secondary species was investigated.

Results

The first species of artiodactyls, which appeared in the grounds of the NPP, was the red deer of hybrid origin, bred in the "Askania Nova" Reserve (Salgansky, 1962; Salgansky, et al., 1963; Volokh, 2016). In consequence of a random mating of various subspecies, an original form emerged, with adaptation to conditions of dry steppe. The animals easily endure absence of woody forage, feeding only on grass plants. In the view of A. A. Salgansky (1962, 1963), the hybrids are very similar to the maral (*Cervus elaphus sibiricus* Severtzov, 1873), but they have a somewhat different exterior and a specific behaviour. However, V. I. Kryzhanovsky (1965) considered that morphological traits of hybrid deer are inconstant, and their population is genetically heterogeneous, which does not justify distinguishing this form as a separate subspecies of *Cervus elaphus askaniensis*, as suggested by A. A. Salgansky (1965).

The first 3 animals (1 male and 2 females) of hybrid individuals of the red-deer were brought to the Biryuchyi Ostriv Spit in 1928. According to the *founder effect* (Mayr, 1942), number of the initial group was too small to provide genetic variability and, consequently, rapid increase of population. Increase in deer numbers during the next decade was gradual, but constant, and reached 60 individuals at the outset of the Second World War. During the years of the occupation, number of the animals fell almost by half, which obliged to carry on the work for their acclimatization. For this purpose, 12 females of the Askanian Steppe deer were brought to the peninsula from "Askania Nova" reserve in 1946, and 4 males — in 1951.

Since the beginning of 50s and to the end of 60s of the past century, the deer growth curve resembles a theoretical exponential curve (fig. 1), where two depressions can be observed, which correspond to harsh winters of 1953–1954 and 1968–1969.

Death of weakened and old animals occurred mainly due to overcooling caused by cold winds, especially harsh because of the lack of trees. Starvation was not the cause of death of ungulates, because throughout the year animals do not need additional feeding (Domnich, 2006 a–c). In particular, harvested hay is not consumed even in winter, despite the significant pasture load. According to P. F. Kaznevsky (1963), who investigated the similar phenomenon in the Voronezh Nature Reserve, in the absence of natural enemies, climatic disasters can act as factors regulating the high density of ungulates population.

In the late 60s and early 70s of the last century, the population of the red deer exceeded 1100 individuals, where after it gradually decreased to almost 600 individuals.

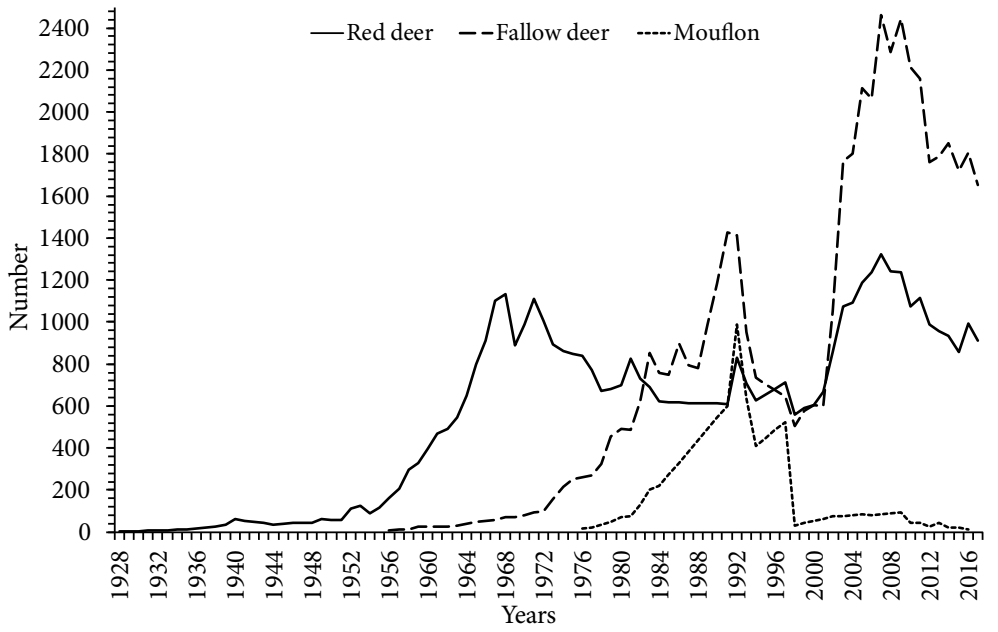

Fig. 1. Dynamics of quantity of the hoof-animals in the Azov-Syvash National Nature Park in the course of 1928–2018.

A significant reduction in the number of red-deer during the 80s last century, in our opinion, was caused by several factors.

A commercial shooting of hoof-animals was carried out in Ukraine until the middle of 1990s with the subsequent export of meat products. In some years a share of slaughtered animals amounted to 3–15 % of their total number. Therefore, elimination was equal to annual increase in number of the animals (An instruction …, 2002).

However, it is worth noting that decrease in quantity of the deer occurred against background of increase in numbers of other ungulate species, first of all — the fallow-deer.

For the first time fallow-deer were released in the NPP lands in 1951, in quantity of 9 animals (3 males and 6 females), but almost all of them perished during the harsh winter of 1953–1954 (Babich, Kaminetskyi, 2008; Kaminetskyi et al., 2011; Volokh, 2016). Next attempt to acclimatize the fallow-deer on the peninsula was undertaken in 1956. For this purpose, another 6 animals (3 males and 3 females) were brought. For that time only one animal from the previous group was still alive. This group formed a nucleus for the future population. In 1961, when the fallow-deer was brought to the peninsula for the last time (3 males and 2 females), its local group included already 25 animals. It is worth noting that formation of fallow-deer population happened in the period when number of the red-deer reached almost half a thousand animals.

As well as the red-deer, fallow-deer were brought to the Biryuchyi Ostriv Spit from the Reserve "Askania Nova", where this species had been maintained since 1889 under conditions of long-term inbred selection (Smagol, 2001). Despite signs of degeneration — slightly poor indices of linear measurements and body weight, a significant percentage of deformations in horn structure, frequent occurrence of animals with non-typical colouring (albinos, melanists) etc. — the fallow-deer have adapted successfully to semi-free maintenance and to climatic and feeding conditions of the steppe biotope.

Therefore, finding themselves in familiar landscape and climatic conditions (which are very similar to those in the Reserve "Askania Nova"), the fallow-deer after introduction entered competitive relations with the red-deer, which has similar requirements for feeding and protective properties of lands (Razmahnin, 1978).

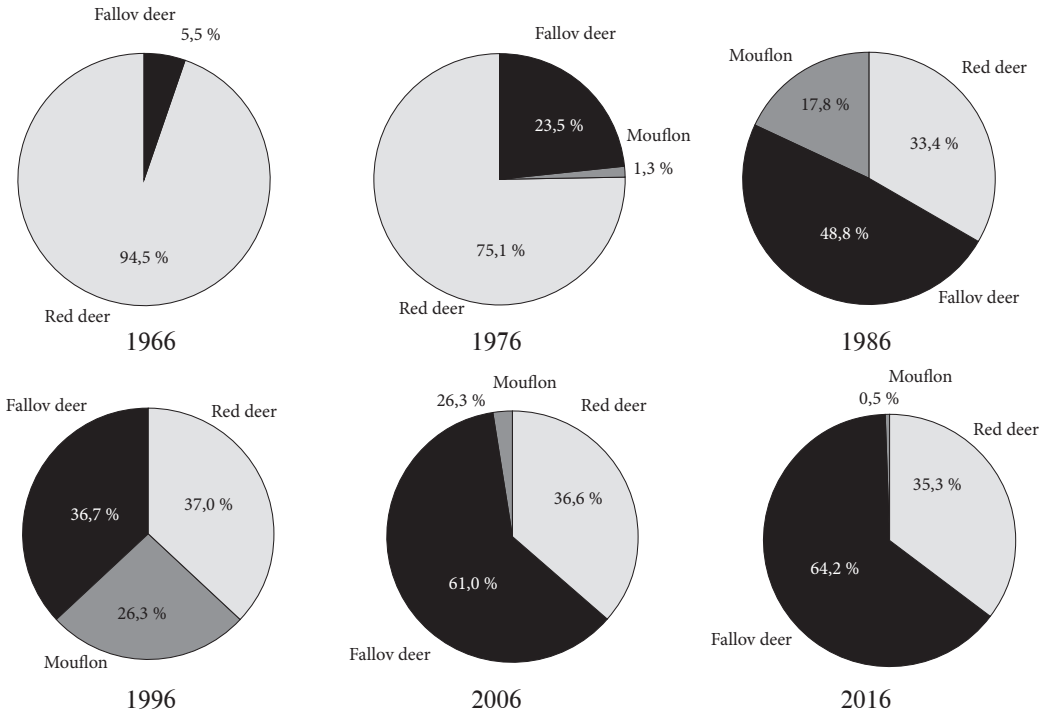

Fig. 2. Change in relationship of numbers of the hoof-animals in the Azov-Syvash NNP.

Analysis of relationship between individual species of the hoofed animals on the peninsula (fig. 2) shows that the fallow-deer in open biotope can successfully compete with the bigger species, and even after some time can occupy a dominant position in the faunistical system.

Under conditions of wood lands (where wood-leafy feeds form a big part of diet for ungulates) trophic zones of the fallow-deer and roe-deer (*Capreolus capreolus* L.) are located at height of up to 1.5 m above ground level because of size of the animals (Drozdz, Osiecki, 1973), that is why the red-deer, as a bigger animal, under conditions of co-existence has some advantages in foraging. In the view of M. A. Lavov (1978), the red-deer consume shoots of trees and bushes till height of 2 m from the surface, therefore a set of forages with lesser nutritive value remains for smaller species. As a result, a so-called qualitative deficiency of alimentation happens. The fallow-deer and roe-deer reproduce less and perish from diseases more often. As a consequence, their number begins diminishing.

In contrast to forest biotope, there are not layered trophic zones in steppe, which negates big body size of the red-deer as a main advantage of the species; trees and bushes are very scarce on the peninsula, and animals feed almost exclusively on grass. Feeding and protective properties of the open steep create equal conditions for both species of the Cervidae family (Domnich, 2006 a, b). Under changed environment conditions, other ecological mechanisms become a driver for competitive ability, which in a completely different way build a social hierarchy of species existing on the same trophic level.

It is known that normally a fallow-deer female bears one fawn. Birth of twins is very infrequent for this species, and even in the most favourable years females who bear twins do not exceed 1–2 % of total number of the females (Steklenev, 1979, 1993). Meanwhile, data from an investigation of genitalia in 19 pregnant female fallow-deer (Smagol, 2001) show a development of two corpora lutea of pregnancy in 3 of them, and investigation of their uteri revealed presence of two embryos. Two of the investigated females had an embryonic mortality of one embryo, placed in a macerated state near the embryo which developed normally. Thus, data of physiologic investigations show that populations of the fallow-deer have a considerable reproductive potential, as almost 16 % of females are theoretically

able to be multiparous. In most cases one of twin embryos perishes at early stages of the development, giving place to the stronger one, perhaps, the first of the originated. Therefore, not every fallow-deer bear female twins till the end of pregnancy, that's why under normal conditions birth of more than one fawn is infrequent in population. This process can be influenced by various factors, both stressing (unfavourable climatic conditions, predator pressing, high density of population etc.) and comforting ones (stable trophic base, availability of free ecological space etc.).

Based on ours observations, number of fallow-deer females bearing twins has considerably increased on the Biryuchyi Ostriv Spit for the last decades. The indicated event, to our opinion, is an ecological mechanism which provides for success in competitive relations with other ungulate species and presently determines a dominance of the fallow-deer in social hierarchy of the species grouping.

It is worth noting that fallow-deer population, despite significant increase rates, for a long time was in equilibrium with other hoofed animal species (fig. 2). It is possible that the reason were scales of actions for stabilization of animal number in the 1990s, carried out in volumes which even exceeded removal of red-deer (in different years — from 17 to 32 % of total number).

Alongside this, the figures 1 and 2 show that significant increase rates of the fallow-deer population began after an abrupt decrease in quantity of the mouflon, and correspondently — after release of a significant part of the ecological space.

Ten individuals of mouflon, brought in 1976 from "Askania Nova" (Kaminetskyi et al., 2011; Volokh, 2016), at once formed on the peninsula a stable population with significant increase rates of their quantity. Literally since the next year quantity of the species began growing exponentially against background of established high indices of quantity of the fallow-deer and red-deer (fig. 1). The mouflon population gained success in the competition owing to a high reproductive ability of the species (Yanushko, 1955), and also thanks to peculiarities of their feeding behaviour.

According K. N. Nikitin's observations, a researcher in the Azov-Syvash Hunting Reserve, the mouflon while grazing bites off grasses till the very root, consequently they use pasture potential better (cited in: V. I. Kryzhanovsky (1965)). In contrast to the mouflon, fallow-deer and red-deer while eating prefer high grasses (biting off only tops), and also prefer those grasses which are about to enter the flowering stage (Domnich, 2006 a–c). Reason for the selective trophic activity of Cervidae is that young shoots of grasses (which usually occupy the highest position) are easier to be digested, and inflorescences contain a high percentage of proteins.

Thus, the fallow-deer and red-deer, against background of trophic activity of the mouflon, reveal signs of *stenophagy*. Besides, an interspecies trophic competition, or to say more precisely — trophic competition between families (as relations at the level of Cervidae and Bovidae families are meant) is grounded on a difference in height of feeding zone. In contrast to forest lands, the vertical line of trophic activity is located at a small height from the earth surface, and, as it was mentioned above, this fact excludes the use of morphometric peculiarities in competitive struggle for trophic resources.

Thus, for 15 years a mouflon population reached the number of almost a thousand animals, posing a real danger of expelling red-deer and fallow-deer, more specialized ecologically. At that time calls were heard about necessity of reducing number of mouflon, which led to a catching and shooting of the animals, removing from 12 to 49 % of the animals in particular years.

It seemed that none ecological factor could stand in the way of "triumphant march" of the mouflon. However, as the years passed, it turned out that animals of this species are very dependent upon influence of climatic factors. In particular, in the spring of 1993 and especially in the spring of 1998 (fig. 1) due to weather abnormalities a disastrous reduction in number of the mouflon happened (Domnich, 2006 d).

In the early spring, along coast of the Biryuchyi Ostrov Spit it was observed an increase in strength and duration of northern and northern-eastern winds, which cause rump waves and lead to a considerable flooding of lowland (firth) part of the peninsula. Night temperature in this period often lowers to negative values, and in particular years (as it happened in 1993 and 1998 years) up to one third of the peninsula area was covered with a layer of ice. As a rule, after partial flooding of the spit a big part of the red-deer and fallow-deer migrate to higher dry places, but no such migrations of mouflons were observed. It is worth noting that major part of the mouflon population was concentrated just in the lowland part of the peninsula, overgrown with reed, where lands with the highest protective properties were located. Thus, territorial conservatism of mouflons became a disadvantage for them, as the animals perished on a massive scale from overcooling, often they just were frozen into ice.

However strange it might be, in the period from 1993 to 1998 years commercial use of the mouflon population did not stop, and after the mass mortality of the animals in 1993 volume of their removal even grew: firstly to 30 %, then to 49 %.

During the mentioned years it was observed a considerable percentage of mortality for the red-deer and fallow-deer, too (fig. 1), but reduction of their number never had consequences as disastrous as those for the mouflon, whose population decreased in the spring of 1998 by 95 %. Nowadays the species is in the state of a deep depression (the group consists of 13 animals), which requires actions for artificial augmentation of their number.

Meanwhile, as mouflons are the most important trophic competitors, decrease in their quantity immediately exerted an effect on the populations of red-deer and fallow-deer, whose increase rates after 1998 resembled one of the acclimatization process stages — "demographic explosion" (Shaposhnikov, 1958; Chesnokov, 1982). Mechanism of this event is grounded on ecological rules which rest upon competition between all the populations of the hoof-animals group.

Results and discussion

Since beginning of introduction into the peninsula ecosystem, the red-deer during a quarter of century was the only significant consumer of the first order (Shilov, 1998). We do not take into consideration other consumers of the primary products (mice and hares), as their total biomass is not significant. On occupying a free ecological niche, the red-deer population expectedly entered the stage of "demographic explosion", that is their number began increasing intensively. However, in the middle of 50s of the past century the fallow-deer was acclimatized on the Biryuchyi Ostriv Spit. A competitor for the red-deer came, and this competitor used a higher reproductive ability as a strategy for ecological survival. Increase rates of the fallow-deer population, in their turn, were terminated by introduction of the mouflon in the middle of 70s, because the latter also has a significant fertile potential, but moreover used the indiscriminateness in feed resources as a competition strategy. In 10 years after the acclimatization, the mouflon became a full-scale member of the biocoenosis, and in another 10 years it posed a weighty alternative to the fallow-deer and red-deer (fig. 2). Thus, "trophic aggresion" of the mouflon became a more efficient ecological strategy as compared with activation of reproductive potential of the fallow-deer.

For a short period (1991–1992) relationship between the populations looked harmonious enough — quantity of all the species grew in parallel (with different rates), preserving a relatively stable dynamics (see fig. 1). Death of the mouflon population in 1998 became an ecological catalyst which caused a "marathon" of augmentation in number of both the species of Cervidae. In the competitive struggle for "freed" trophic resources, the fallow-deer activated again its reproductive potential as a factor suppressing the red deer population.

It is worth noting that in the periods when rates of increase in number lowered (middle of 80s and all the second half of 90s of the past century), there was a considerable percentage of barren females in the fallow-deer population. Thus, "fertile aggression" is reasonable only in regard to the red-deer, which has some common traits with the fallow-deer as for way of life: similar feeding behaviour, similarity of natural cyclicity etc.

On analyzing the formation of both individual populations and general group of the hoofed animals living on the Biryuchyi Ostriv Spit, we deduce that success of their existence depends on anthropogenic influence in a slight manner. It is worth noting that this refers specifically to establishment of populations in terms of time, as their rise as such was a result of human activity. Next formation of the hoofed animal populations in every particular case was stipulated by abiotical environmental factors, as well as by various types of competitive relations. It is worth noting that under conditions of open landscape protective properties of lands are minimized, and interspecies competition is based almost exclusively on trophic links.

Conclusions

Investigation of rates of increase in number shows that the highest level of competitive ability was revealed by the mouflon population, whose sudden reduction in number was a consequence of unexpected climatic disasters. It took only 15 years for the mouflon to augment its number from 15 animals to the level of 1000 (fig. 1). And it happened against a background of already formed populations of the fallow-deer and red-deer. As a comparison, taking 15 animals as a starting point, populations of the red-deer and fallow-deer required 31 years to reach identical values of number.

One can safely say that in the period of prosperity of the mouflon population its trophic activity was a decisive ecological factor (driving force) in the biocoenosis, and competition of the red-deer and fallow-deer looked insignificant against background of this factor. Therefore, the mouflon can be considered an inhibitor for all the Cervidae family. One might guess what cenotic links between individual species would have been and how their interrelation would have looked now, but in the second half of 1980s and first half of 1990s social hierarchy of the species had the following form:

Ovis musimon
↓
Dama dama
↓
Cervus elaphus

Relations between the mouflon and *Cervidae* looks like a typical example of amensalism, like the form of interspecies links when one species suppresses another without experiencing a reverse influence (Reimers, 1991). So mouflon, holding the top of social pyramid, did not "percept" a reverse influence of other herbivorous mammals.

Disappearance of the mouflon from the biocoenosis caused an aggravation of competitive struggle between systematically relative species, in which the fallow-deer exhibited higher ecological plasticity. Meanwhile, relations between the fallow-deer and red-deer do not look like those of *inhibitor* and *amensal*. Both the species have identical feeding behaviour, so upon outnumbering the red-deer, fallow-deer exist in conditions of severe reciprocal competition with them. Starting from the middle of 2000s, number of fallow-deer in the NPP is almost twice as big as that of red-deer. However, according to data from "Project for territorial arrangement of the Azov-Syvash National Nature Park ..." (1995), daily feed requirement of a red-deer on the Biryuchyi Ostriv Spit is 10 kg, while that of a fallow-deer is 5 kg. According to the type of influence, population of both species exert approximately identical loading on grass plants.

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Received 24 October 2018
Accepted 5 March 2019