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GENERAL BIOLOGY

The Effect of the Wolf on the Competition between Ungulates in the Voronezh Biosphere Reserve

A. A. Nikol'skii* and Yu. P. Likhatskii**

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Since reserves are relatively closed areas, they provide favorable conditions for observation of processes occurring in natural ecological systems. The predator–prey interaction and interspecies competition are examples of these processes. The results of ecological monitoring performed in state reserves in the framework of the State Program "Nature Chronicle" have been compiled into a unique database of long-term population dynamics of many dozens of animal species.

In the Voronezh Biosphere Reserve, numerous data have been accumulated on the population dynamics of the wolf and ungulates, including the red deer, roe deer, moose, and wild boar.

The reserve occupies a part of the Usmanskii Bor forest in the Voronezh and Lipetsk oblasts (regions). Its area is about 31000 ha.

We used the data from the *Nature Chronicle* of the reserve to analyze the population dynamics of all five species during the past 32 years (1971–2002). This allowed us to predict the numbers of the wolves and ungulates for the next five years.

The time series of population dynamics began in 1971, because there had been no wolves in this area for the previous two decades. Wolves were specially prevented from spreading in the reserve using predator control methods [1]. The secondary spread of the wolf in the reserve occurred against a background of a general increase in its numbers in the region [2]. Regarding ungulates, the red deer markedly dominated in the early 1970s. Only a few roe deer were observed. The moose and wild boar were common but not abundant.

The most noticeable response to the increase in the numbers of wolves was a dramatic decrease in the numbers of red deer (from 1544 to 67 animals in 1973 and 2001, respectively) and an equally rapid increase in the numbers of roe deer (from 10 to 671 in 1971 and 1997, respectively). The numbers of mooses and wild boars did not change so dramatically. It varied around a certain average level (figure). (To exclude secondary peaks, the curves shown in the figure were smoothed using three-point steps).

The relationship between the numbers of wolves and red deer was the strongest. The statistically significant correlation between their numbers was negative ($r = -0.86$); i.e., an increase in the numbers of wolves caused a decrease in the numbers of red deer. The correlations of the numbers of wolves with the numbers of the other three prey species were positive and also statistically significant ($p < 0.01$ in all four cases) (Table 1). This leads us to the paradoxical conclusion: the more abundant the predator, the more abundant the prey (roe deer, mooses, and wild boars in the given case). The relationship between the numbers of wolves and roe deer was the strongest positive correlation ($r = +0.85$). The only possible explanation of this unexpected phenomenon is that wolves create favorable conditions for the roe deer by "eliminating" its main competitor, red deer. Apparently, wolves preferred red deer because the latter was the prevalent ungulate species in the reserve in the early 1970s, when wolves reappeared there. Conversely, roe deer were extremely rare in this area when wolves began spreading there [1]. The numbers of mooses and boars remained relatively low. As a result, wolves specialized in hunting the red deer, the most abundant and available prey. For example, in 1971, when wolves appeared in the reserve, the total number of red deer (1378) was 3.8 times larger than the total number of the other ungulates (366) [3].

The strong negative correlation between the numbers of red deer and roe deer ($r = -0.89$) (Table 2) suggests that the numbers of red deer are controlled not only by wolf predation, but also by competition with roe deer. The weak relationships of the numbers of red deer with those of mooses ($r = 0.63$) and wild boars ($r = 0.57$) suggest that these species interact insignificantly.

Different factors may make the red deer a weaker competitor. For example, the spatial distribution of red deer in the reserve had changed by the time when wolves spread there. In the 1940s, red deer spent winter in the center of the reserve. In 1970–1979, only 30% of

* *Faculty of Ecology, Peoples Friendship University, Podol'skoe sh. 8/5, Moscow, 113093 Russia*

** *Voronezh Biosphere Reserve, st. Grafskaya, Voronezh oblast, 394047 Russia*

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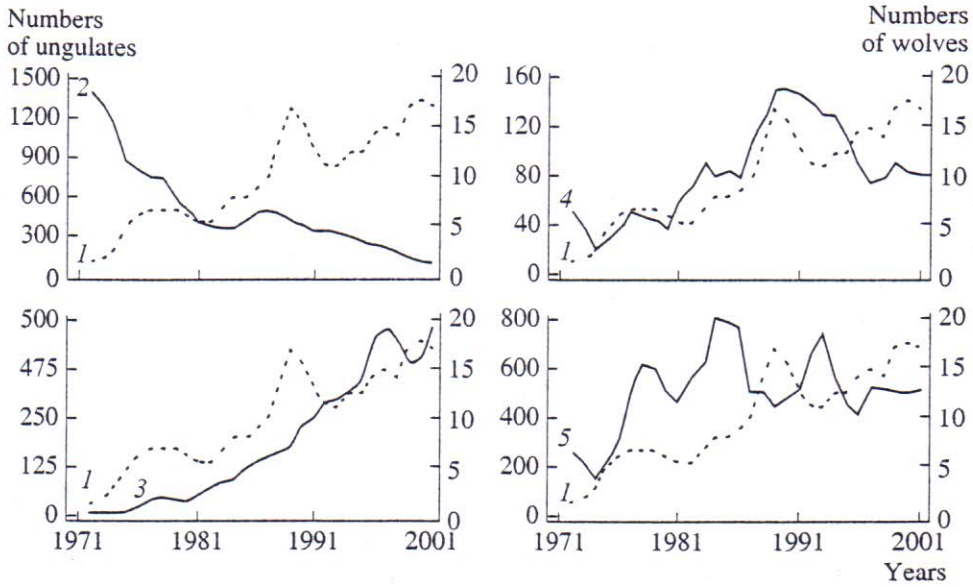

Long-term population dynamics of (*1*) the wolf, (*2*) the red deer, (*3*) the roe deer, (*4*) the moose, and (*5*) the wild boar in the Voronezh Biosphere Reserve.

the population remained there, whereas the others moved to the periphery of the reserve. The main reason was that red deer began to feed on beet roots (that were not harvested or left in stacks on the fields), silage, etc. By the late 1980s, the numbers of red deer decreased more than twofold. The spatial structure of the population remained the same, exhibiting the compact distribution typical of deer (the aggregation indices at the periphery and in the center were 10.8 and 5.7, respectively). The low numbers of red deer, together with the heterogeneous spatial distribution, ensured even more favorable conditions for roe deer in terms of the use of the area [4].

It should also be taken into account that, in contrast to the red deer population, the populations of the roe deer, moose, and boar are aboriginal. By the late 19th century, there were no red deer left in the Central Chernozem forest–steppe except for those kept in menageries. One of the menageries belonged to the Princess of Oldenburg. Red deer were brought there from Germany. In 1917, the menagerie was destroyed, and the deer ran away to give rise to the modern red deer population of the Voronezh Biosphere Reserve [5]. Possibly, the ecological valence of the accidentally formed red deer population is lower than those of aboriginal populations of other ungulates and cannot compete with them. Earlier, red deer flourished because additional feeding was practiced in the reserve [6].

The numbers of ungulates in the reserve are also affected by various factors that we did not take into account, such as poaching, epizootics, regulation activities, weather, and feeding conditions.

The drastic reduction in the numbers of the main prey will inevitably force wolves to hunt other ungulates, including roe deer. This is indirectly confirmed by the changes in the trend of the roe deer population dynamics in recent years (figure, curve *3*). The numbers of mooses and wild boars (figure, curves *4* and *5*, respectively) tend to change periodically; however, the periods of the changes are different for different species.

It was earlier suggested (without a substantiated prediction) that red deer would disappear from the reserve within several years unless the numbers of wolves were artificially regulated [7].

However, prediction is necessary for making the decision as to whether humans should or should not interfere in ecological systems. The potential of the prediction itself should also be estimated before the predicted event occurs. This potential may be estimated, with some limitations, by predicting the event that has already occurred. We call this a "retrospective" prediction.

Table 1. The relationships between the numbers of the predator (the wolf) and preys (ungulates) in the Voronezh Biosphere Reserve from 1971 to 2002

Species	r	R^2, %	Model (regression equation)*
Red deer	−0.86	74.8	$N_U = 1344.28 - 410.111 \ln N_W$
Roe deer	0.85	71.8	$N_U = 4.95484 N_B^{1.47147}$
Moose	0.57	32.7	$N_U = 12.1854 + 24.1072\sqrt{N_W}$
Wild boar	0.47	21.8	$N_U = 249.353 N_W^{0.292961}$

* N_U is the numbers of ungulates; N_W is the numbers of wolves.

Table 2. The relationships between the numbers of red deer and the numbers of roe deer, mooses, and wild boars in the Voronezh Biosphere Reserve from 1971 to 2002

Species	r	R^2, %	Model (regression equation)*
Roe deer	–0.89	79.1	$N_D = 1625.39 - 242.812\ln N_X$
Moose	0.63	40.1	$N_D = 177.8 + 19847.9/N_X$
Wild boar	0.57	32.1	$N_D = 168.458 + 134635.0/N_X$

* N_D is the numbers of red deer; N_X is the numbers of the competitor.

Table 3. The "retrospective" (1998–2002) and "prospective" (2003–2007) predictions of the numbers of wolves and ungulates in the Voronezh Biosphere Reserve. The results of the censuses performed from 1998 to 2002 are shown in parentheses

Year	Species				
	wolf	red deer	roe deer	moose	wild boar
1998	16(15)	206(162)	391(400)	66(89)	521(517)
1999	16(12)	194(134)	408(251)	74(91)	493(431)
2000	15(24)	182(103)	425(496)	80(93)	484(573)
2001	14(17)	171(67)	442(450)	84(68)	483(498)
2002	13(10)	160(102)	460(499)	88(84)	486(459)
2003	12	112	474	84	429
2004	9	103	492	84	413
2005	9	96	509	84	405
2006	9	89	526	84	400
2007	9	83	544	83	397

We used the method of time series (the STATGRAPHICS applied software package) to predict the known population dynamics of wolves and ungulates in the Voronezh Biosphere Reserve from 1998 to 2002. Of all possible solutions, we chose the one for which the difference between the predicted and actual values was the smallest. Then, we used the same type of solution to obtain a "prospective" prediction for the next five years (from 2003 to 2007). Thus, we used the time series for 27 years (from 1971 to 1998) and 32 years (from 1971 to 2002) for the "retrospective" and "prospective" predictions, respectively. Table 3 shows the results.

The prediction may be affected by a change of the prediction model with time [8]. In the given case, the model will be changed when wolves turn to another prey and the pattern of the competition between ungulates changes. However, the prediction is short-term (five years), which allows us to hope that the error of the "prospective" prediction does not exceed the error of the "retrospective" one. The deviation of the "retrospective" prognosis from the results of observations (Table 3) is comparable with the error that is typical of census methods.

According to our prediction, the ecological system of the Voronezh Biosphere Reserve will come to a relatively steady state within five years: (1) the wolf population size will stabilize at the level of about ten animals; (2) the numbers of red deer will remain low throughout this period; (3) the numbers of roe deer will continue to grow gradually; (4) the numbers of mooses will remain stable; (5) the numbers of wild boars will gradually decrease; and (6) probably, the wild boar and moose will become the main preys of the wolf.

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