Analysis of Survival of the Red Fox (*Vulpes vulpes* L.) at the Phases of Population Growth and Decline

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Abstract—Changes in the survival parameters of the red fox were analyzed at different phases of the population cycle. It was found that the survival rate in all age classes, including newborns, drastically increased at the phase of population growth. The relationship between the general mortality rate and population size was determined. A hypothesis concerning the mechanism of these changes in the general mortality rate is suggested.

Key words: survival, fecundity, dynamics, numbers, population, red fox.

The dynamics of an isolated population is a result of the interaction between two population parameters, birthrate and mortality rate. Detailed data on changes in these parameters are necessary for understanding the mechanisms of fluctuations in population size. Both increase and decrease in population size may result from changes in only one parameter in the entire population or even in a structural group within the population. To date, we cannot unambiguously determine what actually causes the growth or decline of a population: changes in survival, fecundity, or both.

As far as I know, ichthyologists were the first to analyze the animal survival curves as related to age (for review, see Biverton and Kholt, 1969; Ricker, 1979). This method of studying population structure has seldom been applied to terrestrial vertebrates with relatively long life spans. For example, Deevey (1947, cited from Odum, 1975) obtained survival curves for the Dall's sheep. Later, this method was used when studying the populations of the New Zealand tahr (Caughley, 1970), the red deer (Lowe, 1969), African ungulates and proboscidians (Spinage, 1972), and (in a modernized form) the wolf (Smirnov, 1983). This method is rarely applied to large terrestrial vertebrates, because it is difficult to determine age in long-lived animals; the very possibility to estimate it accurately only appeared after the studies by Smirnov (1959) and Klevezal' and Kleinenberg (1967).

The ultimate practical goal of studying the red fox, as well as any species that is used by man, is to develop the optimal exploitation strategy. In the case of the species that have been exploited for a long period of time and have not disappeared, the development of this strategy requires data on the spontaneously forming relationship between the rate of animal removal from the population and the size of this population.

The rate of removal can be estimated from the general mortality rate (according to Ricker, 1979). It is interesting to determine whether mortality remains constant or changes depending on the population growth rate. Theoretically, we may expect several consistent patterns of changes in the removal rate, depending on changes in population size. Naturally, the numbers of animals killed during the entire population cycle will be different for different patterns.

I attempted to analyze changes in the estimations of fecundity and mortality (and the inverse value, survival) in fox populations during the entire population cycle.

MATERIALS AND METHODS

The materials of this study were carcasses and skulls of red foxes (*Vulpes vulpes* L.) obtained from trappers in different years. I used data on a total of 1598 foxes. During five trapping seasons (from 1976–1977 to 1980–1981), 839 fox carcasses were collected in the Sverdlovsk, Kurgan, and Tyumen oblasts (hereinafter, this whole region is called Transural). To study the population structure and fecundity of foxes from Kirov oblast, I used the same material that was earlier used in studies performed in collaboration with Solomin (Korytin *et al.*, 1978; Korytin and Solomin, 1980; etc.). The population structure was analyzed on the basis of data on 759 fox carcasses collected during nine trapping seasons (from 1966–1967 to 1974–1975). Hereinafter, this region is called Cisural.

The fecundity of foxes was estimated from the number of embryos and placental spots. When calculating the average fecundity, the numbers of the spots and embryos were matched with respect to the dates of cub birth. When estimating the ecological fecundity (m_x), I assumed that the sex ratio at birth was 1 : 1.

The age of the animals was determined according to Smirnov (1959) and Klevezal and Kleinenberg (1967). Preliminarily, the greatest width of the canal of the fang

and the width of the fang cross section in the widest part were measured. To identify the animals born in the current year, I plotted the distribution of teeth with respect to the relative width of the fang canal expressed in percents. As a rule, there was a gap between these distributions for young and adult animals, which was between the relative width of 30 and 40%. The animals in which the width of the fang canal was more than 41% were considered subadults (under one year of age), and the others, adults. To determine the ages of the latter accurately, the method of Klevezal and Kleinenberg had to be used. The possibility to determine the age of adult animals to an accuracy of one year by counting the layers of tooth cementum in the fang was confirmed by the results of measurements made in animals with known dates of birth, including foxes (Jensen and Nielsen, 1968; Maekawa et al., 1980) and other species of the canine family (Klevezal and Kleinenberg, 1967; Linhart and Knowlton, 1967; Shilyaeva et al., 1975; Grue and Jensen, 1976). The age of adult animals was determined using the standard method (Klevezal and Kleinenberg, 1967) with some modifications (Korytin, 1984).

The population growth rate (r) was estimated according to Caughley (1979):

$$r = \frac{\sum Nt - (\sum N)(\sum t)/n}{\sum t^2 - (\sum t)^2/n},$$

where N is the natural logarithm of the absolute or relative population size, t is the ordinal number of the year, and n is the number of years.

I only considered two periods of the entire cycle of population size, growth, and decline. In population studies, the entire cycle is routinely divided into four phases: growth, peak, decline, and depression. I intentionally excluded the peak and depression from consideration, because I believe it incorrect to distinguish these phases when estimating the population size at one-year intervals. The peak and depression phases should be distinguished based on one condition: the rate of population growth should be zero at these phases. If these phases exist at all, they are considerably shorter than one year, and one year is a standard interval typically used when analyzing population dynamics in vertebrates. A strictly steady state is usually not observed in natural populations.

The material from the Cisural region was divided into two periods: period I, from 1966 to 1970, and period II, from 1971 to 1973. These intervals differed from each other in the rate of population growth. The population growth rate in the Cisural region was estimated based on absolute numbers of foxes obtained from summary tables (according to Smirnov, 1964) separately for females and for the entire population. In the Transural region, only the data on the entire population were used, because the growth rate was estimated on the basis of estimated relative numbers, and it was

impossible to estimate the number of females in the population.

Relative numbers of foxes (the mean value on a five-grade scale) were obtained by interviewing 30–80 trappers yearly. Pooled data on two spatially isolated groups were assumed to represent the entire cycle of population size (population growth in the Transural region and population decline at a varying rate in the Cisural region), assuming that changes in population parameters with time were not population-specific.

The methods of estimating survival that were proposed by Caughley (1979) could not be applied to our data without some modifications. Therefore, let us consider in more detail the estimation of survival in the case where the age distribution in a sample obtained during one trapping season is regarded as the distribution of the age of death in a cohort. Note that this distribution will not fit the distribution of the age of death in a cohort without preliminary transformations unless the population growth rate has remained zero for a sufficiently long period of time.

The estimation of survival at the age x (l_x; all designations are taken from Caughley, 1979) may be obtained by several methods. If the data on killed foxes indicate a constant survival rate (p_x) in different age classes of the sample, survival may be calculated without long preliminary transformations. It is enough to correct the size of the age class 0+ by Smirnov's formula (Smirnov, 1983). The calculation is more complicated if no preliminary assumptions are made as to the pattern of the relationship between survival rate and age, and fecundity (m_x) is analyzed along with survival. Typically, these estimations are not obtained for the same moment of time. For example, in our case, the fecundity was estimated from placental spots, whereas the number of young foxes below one year of age could only be estimated on the basis of data on killed animals. In this case, the sum $S_x m_x$ (where S_x is the age distribution expressed in proportions of the size of the first class) will be distorted due to the possible or regular death of the cubs in the period between birth and about six months of age.

I do not know about any estimations of natural mortality among young foxes obtained by an independent method; therefore, to perform the calculations correctly, it is necessary to calculate the size of the zero age class. Caughley's method 6 (Caughley, 1979, p. 149) cannot be used without modifications, because, in this case, the estimations of the *numbers of animals* in other age classes are required to calculate the size of the zero class, whereas we only have estimations of mortality. To transform them into the estimations of numbers, let us use Deevey's method (method 5 according to Caughley, 1979, p. 148) without preliminary correction for e^{rx}. The sizes of age classes obtained by this method correspond to the beginning of the trapping season. This important circumstance will subsequently simplify the estimation of natural mortality among young foxes.
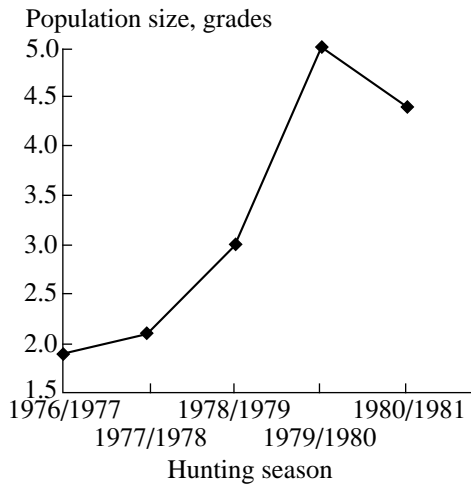
Population size, grades

Fig. 1. Red fox population dynamics in the Cisural region.
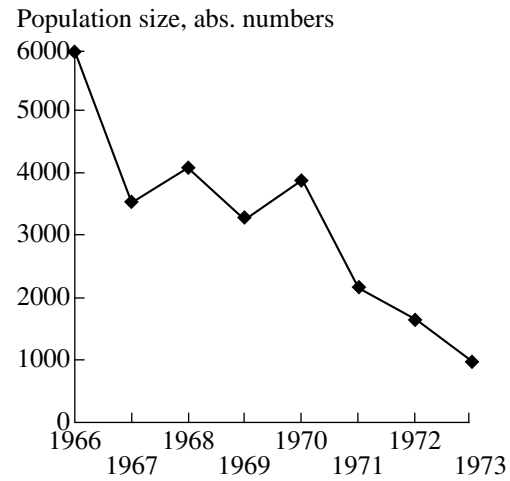
Population size, abs. numbers

Fig. 2. Red fox population dynamics in the Transural region.

The numbers obtained are multiplied by m_x. Although foxes become sexually mature and usually reproduce at age 0+, the value of m_x for 0+ females should be multiplied by the number of 1+ females, m_x for 1+ females, by the number of 2+ females, etc., because only the females that survive through the hunting season will actually contribute to the total number of newborn foxes. After the size of the zero age class is calculated, those of the remaining classes are corrected for e^{rx}, a demographic table is obtained, and the resultant l_x value is assumed to be the survival rate.

This method of estimating survival rate is similar to the methods proposed by Caughley; however, it is not actually identical to either method 5 or method 6; this is why I have described it above in more detail.

When analyzing the distribution of the sizes of age classes, I proceeded from Smirnov's (1983) assumption that the decrease in the sizes of age classes of adult animals follows a geometric progression, i.e., the survival rate of adult animals remains constant. Geometric progression is often used to describe the decrease in the sizes of age classes (Biverton and Kholt, 1969; Seber, 1973; Ricker, 1979). Biverton and Kholt (1969) believe that the coefficient of mortality caused by hunting is proportional to the intensity of trapping. I also made this assumption, as well as an additional assumption that the natural mortality of the animals at the age when they become an object of hunting was negligible. In a study performed in North America (Storm *et al.*, 1976), foxes were labeled, released, and trapped again. The results of these experiments demonstrated that trapping and shooting are the main factors of mortality among foxes; as many as 90% of returns were accounted for by trapped and killed animals. Since I could not correctly estimate the natural mortality of adult foxes, I assumed it to be zero and did not subject it to further analysis.

The removal rate was estimated from the summary table (Smirnov, 1964, 1967) as the ratio between the amount of foxes killed during the hunting season and the population size (resource for hunting) in the given year. This corresponded to Ricker's (1979) estimation of the biostatistical coefficient of exploitation for the

Table 1. Demographic table for female foxes from the Transural region. Age distribution is corrected for population growth rate

Age class	Distribution of ages at death, abs. numbers	Estimated sizes of age classes	Survival (l_x)	Fecundity (m_x)	Survival rate (p_x)
0		498.8	1.000	0.0	0.747
0+	184	372.5	0.747	0.0	0.435
1+	41	162.1	0.325	2.69	0.710
2+	18	115.2	0.231	2.93	0.697
3+	17	80.3	0.161	3.21	0.514
4+	4	41.3	0.083	4.44	0.692
5+	2	28.6	0.057	4.44	0.696
6+	1	19.9	0.040	4.44	0.693
7+	1	13.8	0.028	4.44	

Table 2. Demographic table for female foxes from the Cisural region I. Age distribution is corrected for population growth rate

Age class	Distribution of ages at death, abs. numbers	Estimated sizes of age classes	Survival (l_x)	Fecundity (m_x)	Survival rate (p_x)
0		276.4	1.000	0.0	0.580
0+	113	160.2	0.580	0.0	0.330
1+	34	52.9	0.191	1.34	0.437
2+	15	23.1	0.084	2.00	0.485
3+	7	11.2	0.041	1.79	0.545
4+	2	6.1	0.022	2.68	0.721
5+	4	4.4	0.016	2.68	0.500
6+	1	2.2	0.008	2.68	0.454
7+	0	1.0	0.008	2.68	
8++	4	0.9	0.004	2.68	

Table 3. Demographic table for female foxes from the Cisural region II. Age distribution is corrected for population growth rate

Age class	Distribution of ages at death, abs. numbers	Estimated sizes of age classes	Survival (l_x)	Fecundity (m_x)	Survival rate (p_x)
0		270.6	1.000	0.0	0.353
0+	91	95.6	0.353	0.0	0.246
1+	29	23.5	0.087	1.75	0.323
2+	11	7.6	0.028	2.41	0.382
3+	5	2.9	0.011	2.90	0.448
4+	5	1.3	0.005	2.91	0.385
5+	3	0.5	0.002	2.91	0.300
6+	2	0.15	0.0006	2.91	0.200
7+	1	0.03		2.91	

entire resource. The removal rate was also calculated as the mean mortality rate in cohorts during the given hunting season. The estimation of the removal rate based on the demographic table was calculated as the geometric mean of the mortality rates at ages 0+ and 1++ determined from the series corrected for the population growth rate.

RESULTS AND DISCUSSION

The red fox is a relatively fertile and long-lived species. One female may bear five to seven cubs (which corresponds to 2.5–3.5 females, on average). The average life span of the red fox is 5–6 years; the oldest fox out of 2082 animals in our sample was 11 years old. Let us consider the population structure and removal rates in each of the three cases compared: in the Transural region and in the Cisural region during periods I (1966–1970) and II (1971–1973).

Judging from relative estimations, the numbers of foxes in the Transural region in 1976 were low (Fig. 1). This was followed by a dramatic population growth. The population size peaked in the hunting season of 1979–1980 and decreased by 15–20% by the season of

1980–1981. The population growth rate was 0.33; in other words, the population increased by a factor of 1.4 ($e^{0.33}$) every year. Knowing the population growth rate, we may transform the summary age distribution for the last four years so that it will allow us to estimate the "true" survival (Table 1). The survival of cubs (age 0) was 0.75, and the survival rates of young (0+) and adult (from 1+ to 7+) animals were 0.44 and 0.67, respectively (the latter value is the geometric mean of survival rates for all adult age classes). The removal rate calculated from survival was 0.44.

The estimations of population sizes suggest that the entire period when the material was collected in the Cisural region may be subdivided into two parts according to the population growth rate (Fig. 2), which was $r = -0.12$ and $r = -0.43$ during the first and second periods (Cisural region I and Cisural region II, respectively).
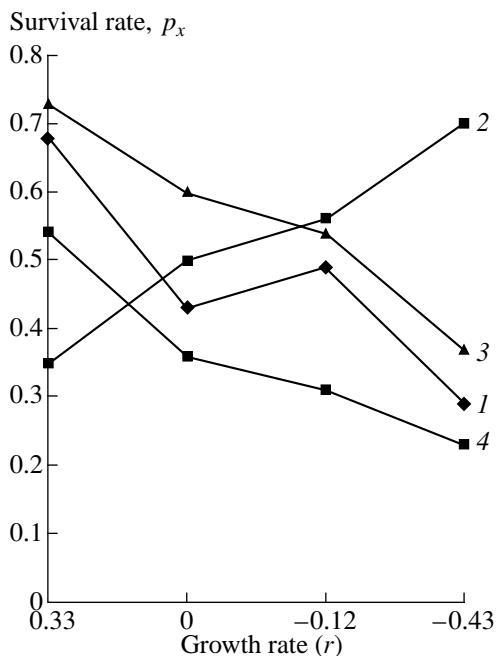
Tables 2 and 3 show similar estimations of survival and survival rate of female foxes in the Cisural regions I and II. Note that the survival of cubs was 0.58 in Cisural region I (versus 0.75 in the Transural region) and 0.35 in the Cisural region II. In other words, this

Table 4. Demographic table for a conventionally steady-state population with the average fertilities actually observed in the Transural and Cisural regions

Age class	Survival (l_x)	Fecundity (m_x)	$l_x m_x$	Survival rate (p_x)
0	1.000	0.0		0.52
0+	0.515	0.0		0.33
1+	0.170	2.32	0.394	0.52
2+	0.089	2.80	0.249	0.57
3+	0.051	2.97	0.152	0.47
4+	0.024	3.73	0.090	0.63
5+	0.015	3.73	0.056	0.60
6+	0.009	3.73	0.034	0.56
7+	0.005	3.73	0.019	
			$\Sigma = 0.994$	

value was minimal during the period of more pronounced population decline and maximum at the phase of population growth.

This pattern of changes in the survival of cubs at different phases of population dynamics suggests that the cub survival is affected by extrapopulation factors to a greater degree than by internal factors. Similar changes in the mortality of young animals at the phases of population growth and decrease were observed in the red deer (Carrol and Brown, 1977) and common vole under experimental conditions (Walkova and Bujalska, 1977).

Fig. 3. Changes in the survival rates for different age classes at different rates of red fox population growth: (*1*) survival of cubs (from birth to the age of six months), (*2*) survival of subadults, (*3*) survival of adults, and (*4*) removal rate.

The removal rates in the Cisural regions I and II were 0.57 and 0.71, respectively.

Thus, the removal rate in the growing population (0.44) was lower than in the population whose size decreased; the smaller the population size, the higher the removal rate.

The population growth rate seems to be largely affected by the intensity of hunting. Let us consider this relationship in more detail. The beginning of population growth in the Transural region coincided with a drastic (almost twofold) increase in fecundity; hence, the population size considerably increased by the next trapping season. Beginning from that season, the removal rate was lower than it was during the decrease in the population size. For example, in the season of 1976–1977, when the population size was lower than 2 grades on the scale of expert estimation, the mean number of placental spots in all females was 4.19 ± 0.62; in the next season (1977–1978), the population size was 2.32 grades, and the average number of placental spots was 8.33 ± 2.03. Apparently, trapping did not significantly hamper population growth during the growth phase, compared to the phase of decline.

Based on the resultant three series of survival (Tables 1–3), we may calculate the case of a conventionally steady state of the population, if we assume that the fecundity is an average value for all three cases. After averaging the series of survival (l_x) and fecundity (m_x), I found that a population with these parameters of birth and mortality will grow at a rate of about $r = 0.083$. This estimation was obtained using the formula (Pianka, 1981) $r = \ln R/T$, where $R = \sum l_x m_x$ and $T = \sum x\, l_x m_x$. After the series of survival was corrected for $r = 0.083$, I obtained $R = 0.994$ (Table 4). Thus, the pure rate of reproduction (R) calculated according to Pianka (1981) was almost equal to unity; in other words, the population with these values of survival and fecundity will remain constant from year to year.

Table 5. Average durations of the periods of increase and decrease in the number of fox pelts obtained by trappers, years

Phase	Oblast (administrative region)				
	Sverdlovsk	Perm	Chelyabinsk	Kurgan	Tyumen
Increase	1.45 ± 0.19	1.42 ± 0.20	1.60 ± 0.16	1.86 ± 0.34	1.44 ± 0.24
Decrease	1.78 ± 0.32	1.55 ± 0.28	1.89 ± 0.31	2.00 ± 0.26	1.50 ± 0.27

The survival of cubs from their birth to the age of about six months (when they become an object of hunting) was 0.52, i.e., every other newborn survived in the conventionally steady-state population. This value also includes embryonic mortality, as fecundity was estimated from the number of embryos and placental spots. Immigration and emigration may affect this estimation to a greater extent than other estimations, because it is known that young foxes that begin living independently of their parents are more inclined to migrate than adult foxes (Chirkova, 1955; Ables, 1965; Lund, 1967; Jensen, 1968).

The survival rate of young foxes (age 0+) was 0.33, i.e., even lower than the survival rate of cubs. The survival rate of adults (the age interval from 1+ to 7+; $p_x = 0.56$) was higher than that of young animals. This was not surprising, because young animals are known to be removed from the population at a higher rate than adults (Korytin and Smirnov, 1978). The rate of removal (the geometric mean of mortality rates for all age classes that are objects of trapping) for a steady-state population with these values of fecundity is 0.54, i.e., the population size will remain the same if 54% of the animals will be removed every year. Figure 3 shows the changes in the survival rates in different age groups and the general removal rate. At the phase of population decline, the survival rate decreased in all age groups. At the phase of population growth, the survival rate increased (and the mortality rate respectively decreased) also in all age groups.

Thus, population growth was ensured by a drastic increase in survival in all age groups and an equally drastic increase in fecundity. I think that the most interesting finding was the considerable decrease in the numbers of subadult foxes in the period before trapping (age class 0). An increase in the absolute amount of the foxes killed during the hunting season was accompanied by a decrease in the general mortality rate.
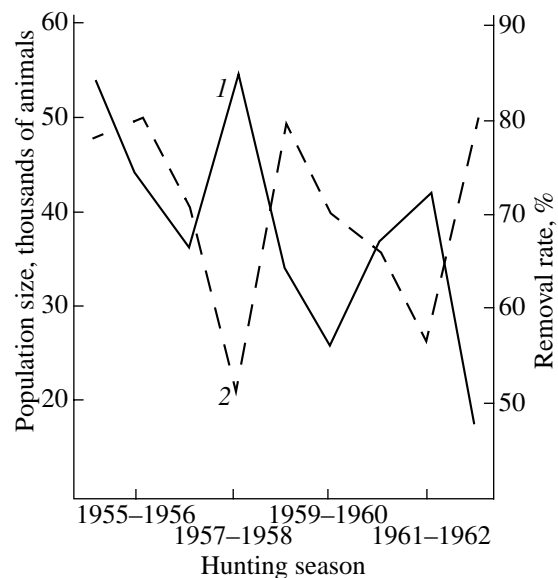
The analysis of the intensity of hunting in the Cisural region, based on summary tables, demonstrated that hunting was excessive at the phase of population decrease; in other words, the removal was greater than the population growth. During period II, there was a compensatory (Korytin, 1983) increase in the fecundity of foxes in the Cisural region (Table 3, column m_x); however, this increase did not completely compensate for the loss due to the high mortality.

Let us assume that, in the absence of hunting, the sizes of fox populations exhibit almost uniform cyclic changes, and let us not take into account the specific causes of the population growth and decrease. Then, these different trapping pressures at different stages of population dynamics should have the following consequences.

Due to the lower pressure at the population growth phase, the population size should reach its peak more rapidly than the same population reaches the depression phase. This will result in differences between the durations of the periods of increase and decrease in the amount of fox pelts stored, with periods of the increase in the number of pelts obtained should be shorter than the periods of its decrease. A large amount of data on the numbers of fox pelts obtained in five regions of the Urals for 35 years is available, which allows us to test the aforementioned suggestions (Table 5). Indeed, the mean period of the increase in the number of pelts obtained was somewhat shorter than the mean period of the decrease in all regions. The absolute differences were small but significant ($P = 0.95$), according to the results of the sign test (Gubler and Genkin, 1973).

I used the data reported by Smirnov (1964, 1967) to find a similar relationship between the removal rate and population size in the Arctic fox. As is clearly seen from

Fig. 4. Population dynamics and removal rate of the Arctic fox in the Yamal Peninsula (according to Smirnov, 1967): (*1*) oscillations of population size, (*2*) changes in the removal rate.

Fig. 4, the removal rate only increased in the next year after the peak of population size; it changed similarly to the changes in the numbers of animals but was delayed by one year. Shilyaeva (1982) noted that the minimum removal rate in the Arctic fox coincides with the peak of the population size, and the maximum removal rate, with the depression phase.

The following hypothesis may explain the observed pattern of the relationship between the removal rate and population size. Assume that the entire region suitable for hunting red foxes of Arctic foxes is divided into trapping plots, the number of trappers changes little from year to year, and all trappers have the same numbers of traps. In this case, we may also assume that the possible range of changes in hunting pressure has an upper limit. Eventually, trappers adapt to certain average numbers of foxes. Therefore, they set about the same number of traps at the stages of both population growth and population decline, which leads to a decrease in the removal rate in the former case and its increase in the latter case. It is possible that this spontaneous relationship between the oscillations of the population size and the removal rate is characteristic of not only individual populations of red and Arctic foxes, and not only these species as a whole, but also of other species with similar fecundity and mortality parameters that are objects of hunting.

Another obvious conclusion is that, to optimize the process of hunting and increase the total number of animals procured, the hunting pressure should be considerably increased at the population growth phase and decreased at the phase of population decline.

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