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Anderson's mortality model which is based on dividing mortality into vitality-related and vitality-independent constitutents is applied to endangered Armenian leopard population. Analysis of skin yield statistics shows that the leopard population half-life for survival to drop to 50% from the effect of accidental causes (hunting) T_{50a} is 2 years, whereas the population half-life for survival to drop to 50% from the effect of vitality-related causes T_{50v} is 20 years. Much shorter period of T_{50a} indicates the strict dominance of accidental mortality over vitality-related counterpart due to intensive poaching.

INTRODUCTION

Recently Anderson [1] has categorized individual mortality into two classes: that dependent on the past history of the organism and that independent of the past history. The former is designated as a vitality-related mortality where vitality is an abstract holistic property that can be accumulated and lost. An organism's physiological resistance to disease, level of stress, behavior, success and failure in feeding, predator attacks, mating, parental care and habitat choice all are the processes involved in the concept of vitality. In this model, vitality is stochastic (randomly distributed) parameter and mortality occurs if vitality reaches zero. Mortality can also occur independent of an organism's vitality and this will be referred to as a vitality-independent or accidental mortality which includes the harvest of a population (hunting, culling, trapping, etc.) and catastrophic events. In this context, probability of an individual's survival P has been a product of the probability of not dying from vitality-related causes, P_v, and the probability of not dying from accidental causes, P_a, and is expressed as follows:

$$P(t) = P_v(t) \, P_a(t) \qquad (1)$$

Crucial parameters involved in the Anderson's individual-based model of population mortality are the population half-life T_{50v} and the population half-life T_{50a} (both in years) for survival to drop to 50% from the effect of vitality-related and accidental mortality alone, respectively (equations 2 and 3):

$$T_{50v} = V_0^2 / (0.5 - V_0 R) \qquad (2)$$

where V_0 is initial vitality, $yr^{1/2}$ and R is rate of vitality change, $yr^{-1/2}$.

$$T_{50a} = -\lg 0.5 / k \qquad (3)$$

where k is the rate coefficient for accidental mortality, yr^{-1}.

The ratio T_{50a}/T_{50v} provides a measure of the importance of both accidental mortality and vitality-related mortality in the population survival. The shorter the period for survival to slump to its half (T_{50}), the higher value of mortality and the more significant contribution of this kind of mortality to the whole population's demographic pattern. So, if the half-life ratio is above 1, then vitality-related mortality dominates and the ratio below 1 suggests accidental mortality larger that the vitality-related counterpart.

FITTING THE ANDERSON'S MORTALITY MODEL TO REAL DATA

Calculated as a natural logarithm of the skin yield changes in time, the rate coefficient for accidental mortality (hunting) k in Armenian leopards is equal to 0.154 yr^{-1}, hence population half-life required for survival to drop to 50% from the effect of accidental mortality (hunting) $T_{50a} = 2.0$ yrs. At first sight, this value seems to be too small for the species with quite a long period of generation turnover (5 years), but it becomes fully credible under detailed viewing the fact that Armenian population of leopard consists of separate "islands" each being founded by a mature and fecund female. As in many other animals [2], juvenile male cubs show higher mortality than females due to maternal preference of daughters over sons in the rearing process, larger body size of males (up to

50%) and their faster growth and increased nutritional requirements, and survived fully grown females stay within their birth ranges or beside to set up their own groups of the young who will then disperse to the neighboring non-occupied habitats. So, killing of the founder female which was recorded, for example, in 1986 when a pregnant leopardess was shot dead in Khosrov Reserve by a trespasser herdsman may entail rapid disappearance of the whole group and considerable decline of the population survival in about 2 year timespan. As a proof, it should be noted that Khosrov leopard population has vanished in late 1980s and was recorded to re-emerge only in 1992-93 in number of three to four pairs [3].

Anderson has estimated that in homeotherms (birds and mammals) the value of initial vitality V_0 depends linearly on the animal body weight by equation 4:

$$V_0 = 0.69W + 1.91 \quad (r = 0.98, p < 0.001) \tag{4}$$

Using the average leopard body weight commonly applied by the scientists, 45 kg [4], we come to $V_0 = 33$ yr$^{1/2}$.

Similarly, rate of vitality change R depends in homeotherms linearly on the rate coefficient for accidental mortality k as follows (equation 5):

$$R = -(8.41k + 0.34) \quad (r = -0.82, p < 0.001) \tag{5}$$

Using the value of k calculated above for Armenian leopard, we get $R = -1.63$ yr$^{-1/2}$.

Finally, to measure population half-life required for survival to drop to 50% from the effect of vitality-related mortality T_{50v}, we should simply put the estimates of V_0 and R of Armenian leopards in equation 2. By this procedure, we get $T_{50v} = 20.0$ yrs.

Thus, half-life ratio T_{50a}/T_{50v} in Armenian leopard population is 0.1, proving the strict dominance of accidental mortality caused by hunting over vitality-related one (Table 1). Unless the illegal slaughter of local leopards is stopped at all, their number is likely to reach zero much sooner than predicted given the data on current abundance.

Table 1. Comparison of survivorship parameters used in the Anderson's population mortality model in some plants and animals ([1], present study).

Species	Population half-life, yrs		T_{50a}/T_{50v}	Dominance of mortality factor(s)*
	T_{50v}	T_{50a}		
Grass (*Trichachne* spp.)	6.5	5.1	0.8	VR≅A
European buttercup (*Ranunculus acis*)	2.0	10.5	5.3	VR
Sessile rotifer (*Foloscularia conifera*)	0.02	0.3	15.4	VR
Mosquito (*Aedes aegypti*)	0.16	0.8	4.9	VR
South African limpet (*Patella cochlear*)	12.1	4.9	0.4	A
Sockeye (*Oncorhynchus nerka*)	0.07	19.8	280.2	VR
Lapwing (*Vanellus vanellus*)	1.7	5.3	3.1	VR
Field vole (*Microtus agrestis*)	0.7	2.0	2.8	VR
Dall sheep (*Ovis dalli dalli*)	10.9	2.7	0.2	A
Persian leopard (*Panthera pardus saxicolor*)	20.0	2.0	0.1	A
Man (*Homo sapiens*)	68.3	346.6	5.1	VR

Note: * VR - dominance of vitality-related mortality factor(s); A - dominance of accidental mortality factor(s).

In practice, however, the role of vitality-related mortality in Armenian leopard population may be much higher and the half-life T_{50v} may be much shorter than 20 years due to demographic impairments caused by inbreeding (loss of genetic polymorphism or heterozygosity created by kinship mating within the small breeding groups), especially increased juvenile mortality. Although some authors regard the leopard a genetically polymorphic and variable species [5], when living in small kinship-based groups it becomes a subject of considerable inbreeding depression [6, 7]. More specifically, inbred populations show increased juvenile mortality and this phenomenon is well documented in both mammals [8-11] and humans [12].

In Armenia, the leopard population is previously estimated to lose its genetic variation and acquire homozygosity (inbreeding) at a rate 2.5-3% per generation and after approximately 30 generations (150-180 years) it will run down to total disappearance [4]. Probability of the kinship mating in Armenian leopard population squeezed by agricultural lands and human settlements is very high due to its social structure. Grown daughters disperse not far from their mother and their individual ranges fall within the father's territory, so that the father-daughter mating may be quite a common event in the country.

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