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Ecological–genetic approach in modeling the natural evolution of a population: Prospects and special aspects of verification

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ABSTRACT

This study presents a complex approach for modeling the natural evolution of a population in terms of population number and dynamics of the genetic structure. A set of dynamic models that consider various types of natural selection was applied to describe possible mechanisms underlying the formation of existing genetic variations in litter sizes in coastal, inland, and farmed arctic fox populations (*Alopex lagopus*, family *Canidae*, order *Carnivora*). The r–K selection model for uniform population and the models with natural selection were assessed on various life cycle stages in a two-age population. The life cycle of arctic fox was fitted to the population model with two age stages. The different reproductive potentials and survivability of progeny on the early stage of life cycle were genetically determined using the model with a single diallelic gene. A monomorphism was obtained for a considered characteristic in a population of coastal arctic fox with constant food supply. Meanwhile, a polymorphism with cyclic fluctuations in population number and gene frequency was obtained in inland arctic fox populations, which could be due to cyclic fluctuations of prey. In farmed fox populations, the considered gene becomes pleiotropic (defines the survival rate of individuals on early and late stages of the life cycle) because of artificial selection performed by farmers to increase the reproductive success of breeders. The application of an appropriate model (with selection by pleiotropic gene) can be used to determine the elimination rate of low litter size alleles from the farmed populations. The possible applications of the proposed models for formulating and solving optimal control tasks in arctic fox populations are discussed too.

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1. Introduction

The dynamic theory of populations is traditionally considered an adjacent section of theoretical population ecology and population biophysics (Bazykin, 1985; Vol'kenshtein, 1988; Romanovskij et al., 2004). Nevertheless, the main problems associated with the dynamic theory are the description of the nature and mechanisms of the fluctuating (i.e., quasi-periodic and chaotic) behavior of populations. Addressing these issues is important to develop an optimal strategy for utilization of commercial species (optimization of “harvesting”).

Mathematical population genetics, which is another branch of population dynamic theory, has rapidly developed since the 1930s.

With this theory, researchers have developed and investigated several models of evolutionary changes in the genetic structure of populations (Haldane, 1924; Fisher, 1930; Crow and Kimura, 1970; Ratner, 1973); however, these models do not consider the features of population dynamics.

The combination of population-ecological and population-genetic approaches has emphasized two types of problems, which can be resolved using mathematical population genetics.

The first problem is the natural development of studies on evolutionary factors (natural selection), which can change the genetic structure and behavior of population dynamics, as influenced by limited environmental resources (Hanski, 1999). In this regard, the concept of r–K selection was developed; this model considers the struggle for existence as defined by the different strategies of survival at the genetic level. Some genotypic groups rapidly propagate and therefore exhibit a high reproductive potential r (r-strategy), whereas other groups adapt to limited resources and present a high capacity of the ecological niche K (K-strategy). Investigation of evolution in uniform populations by using the concept of r and K selection (MacArthur and Wilson,

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1967; Charlesworth, 1971; Rougharden, 1971; Pianka, 1978) provides novel understanding on the nature of fluctuations in biological population number. Even in a uniform population, various dynamic regimes exist, which ranges from stable dynamics to fluctuations in the population number with a stable genetic structure and simultaneous fluctuations in the genetic structure and population number. Considering the population age structure may provide new insights into the evolution of structured populations.

The second problem is the need to analyze harvest consequences. The concept of the maximum equilibrium catch (Skaletskaya et al., 1979; Abakumov, 1993; Braumann, 2002; Hauser et al., 2006; Cooch et al., 2014) asserts that harvested populations are not located under the same ecological conditions to that of nonharvested populations. Thus, selection conditions and fitness of genotypic groups can change in harvested populations.

The ecological–genetic approach provides wide prospects to study the evolution of natural populations and predict changes related to the anthropogenic effect. However, model verification is laden with serious difficulties. For example, assessment of the considered ecological and genetic parameters requires data on the long-term ecological and genetic monitoring of natural biological populations, but data with sufficient volume and quality are impossible to obtain. Therefore, obtaining even rough estimates by using the models under consideration, which can reveal the main features of population evolution and dynamics, is a necessary step to verify combined theories.

In this work, ecological–genetic models were applied to explain polymorphisms in the populations of arctic fox, which exhibit radically different reproductive strategies at the genetic level. The modeling results obtained from the frame of this approach are applied to this complex natural system, which are necessary to understand and consider ecological–genetic processes for investigating arctic fox populations. A set of previously developed models is extended by models with cyclically varying parameters to consider the cyclical changes in food supply in the continental populations of arctic foxes. A classification of the modified model dynamics is obtained by a numerical study performed in the region of parameters according to the features of a particular inherited trait considered in this population.

2. Evolutionary model of homogenous population

We first introduce and review a theoretical framework previously developed that we will make use of in this study. Zhdanova and Frisman (2005) used a simple model that considers the mechanisms of interconnected changes in the genetic structure and population size induced by the interaction of ecological (i.e., factors that limit the population size growth) and evolutionary (i.e., generally selective) factors; the following assumptions were used: genetic variation is controlled by a single diallelic locus (with alleles A and a), and the phenotype of an individual is strongly determined by its genotype; the population is panmictic; Mendelian inheritance rules are followed; and the related generations of individuals do not overlap. In this case, the result of natural selection may be described quantitatively by assigning the coefficient w_{ij} named as fitness to each genotypic group of individuals (ij). This coefficient (w_{ij}) is the average number of offspring produced by one individual from a genotype class (ij) that survives to the reproductive age (i.e., contributes to the next generation) (Fisher, 1930).

The model of the population dynamics of homogeneous Mendelian diploid organisms can be described as follows:

$$\begin{cases} x_{n+1} = \bar{w}_n(x_n)x_n \\ q_{n+1} = q_n(w_{AA}(x_n)q_n + w_{Aa}(x_n)(1 - q_n))/\bar{w}_n(x_n), \end{cases} \quad (1)$$

where $\bar{w}_n = w_{AA}(x_n)q_n^2 + 2w_{Aa}(x_n)q_n(1 - q_n) + w_{aa}(x_n)(1 - q_n)^2$ is the average fitness of the population in the n th generation, x_n is the population number in n th generation, and q_n is the frequency of allele A in the n th generation.

Ecological limitation is implemented by the dependence of genotype fitness (w_{ij}) decreasing from the population size:

$$w_{ij} = \exp\left(R_{ij}\left(\frac{1 - x_n}{K_{ij}}\right)\right) \quad (2)$$

where R_{ij} and K_{ij} are the Malthusian and resource parameters of the ij genotype, respectively. R_{ij} and K_{ij} characterize the reproductive potential of a genotype and the capacity of the ecological niche, respectively. If the entire population consists of individuals with the ij th genotype, the equilibrium number is K_{ij} . We consider a scenario where different genotypes are advantageous in a large or a small population size; in other words, some genotypes are more fecund, whereas the other genotypes are more fitted to limited resources. Thus far, the suitable strategy for survival during evolution remains unclear.

Investigation of model (1) shows that resource parameters (K_{ij}) determine the direction of natural selection, that is, genotypes with the highest values of resource parameters are fixed in the population and Malthusian parameters (R_{ij}) determine the type of dynamic regime (i.e., stable or fluctuating).

2.1. Role of r - K selection in differentiation of reproductive strategies in coastal and inland arctic foxes

We now implement the previous modeling results to describe the evolution of a natural population. Arctic fox (*Alopex lagopus*, family *Canidae*, order *Carnivora*) is an interesting research subject in terms of the evolution and genetic control of the life history traits of animals. Natural populations of *A. lagopus* inhabit coastal and inland areas, depending on different types of resources available, and considerably differ in their reproductive strategy. Coastal foxes feed on sea birds, fish, seals, and marine invertebrates (Hersteinsson and Macdonald, 1996). The availability of these resources minimally fluctuates from year to year. Coastal foxes produce litters of moderate size yearly. Conversely, inland foxes depend on small rodents, mainly voles and lemmings, whose populations are characterized by cyclic fluctuation (Angerbjörn et al., 1999). In years with low food supply, inland fox population demonstrates a very low rate of reproduction. By contrast, in years when prey species are abundant, female inland foxes can produce up to 16–18 offsprings. The average mean litter size and coefficient of variation are 1.5-fold higher in inland populations (Tannerfeldt and Angerbjörn, 1998a,b; Elmhagen et al., 2000).

Axenovich et al. (2007) performed complex segregation analysis of litter size in the extended pedigree of farmed arctic foxes to gain insights into their genetic basis of reproductive strategy. The analysis demonstrated that the inheritance of this trait can be described within the framework of a major gene model with recessive control of low litter size. The authors (Axenovich et al., 2007) suggested that a system of balanced polymorphism for litter size in the farmed population may have been established in natural populations of arctic foxes induced by adaptation to drastic fluctuations in prey availability.

The dynamics of allele A frequency in populations of arctic fox are evaluated using the r - K -selection model (1). Here, the population age structure is not considered but the effect of the varied success rates in terms of reproduction and survivability is considered in the case of limited life resources. Based on the mode of litter size inheritance discovered by Axenovich et al. (2007), genotypes AA and Aa (dominant traits) produce litters of high sizes, whereas genotype aa (recessive trait) generates low litter sizes.

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