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Genetic polymorphism under cyclical selection in long-lived species: the complex effect of age structure and maternal selection

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Motivation and Aim: The maintenance of genetic polymorphism in heterogeneous environments continues to be a topic of research interest in evolutionary genetics for a long time. Storage effect is known [1] to maintain genetic polymorphism in fluctuating environments via buffering factors limiting the impact of negative selection in temporarily unfavorable environments, thereby avoiding allele extinction. A major buffering factor is overlapping generations due to age (stage)-specific selection. Another type of buffering factors that promote the maintenance of polymorphism are genetic ones, such as natural selection on sex-limited traits, maternal (or paternal) selection, and various maternal genetic effects as well (i.e. genomic imprinting or delayed inheritance) [2]. Despite this framework has a long history and the significant progress has been achieved in understanding the conditions for maintaining genetic variety, the complex effect of the principal buffering factors under study: overlapping generations and genetic (in particular maternal selection) has not been discussed in details. At that, in populations of long-living species, both of these factors act simultaneously and the result of their joint action is not obvious.

Our study basically tries to model a situation demonstrated by arctic fox populations, where the litter size being a major life history trait is a sex-limited female trait [3]. It is influenced by maternal selection with cyclic fluctuations because of oscillations in food abundance [4]. Note, arctic fox is a long-lived species having an age structure. An evolutionary mechanism that promote the maintenance of genetic variation in litter size of this species is not entirely clear.

Methods and Algorithms: We consider the maintenance of polymorphism under the complex influence of maternal selection, age structure, and fluctuating environments. We also consider two models of natural selection in a population with and without age structure [5] and the model of maternal selection in a population without age structure [6] as reference points for the age-structured model with maternal selection.

Results: For a population with non-overlapping generations, the analysis results of the influence of different cycle lengths and the ratio of reproductive potentials of genotypes on maintaining polymorphism turned out to be quite expected. Maternal selection always dilates polymorphism region vs. classic selection. The longer an external cycle, the narrower polymorphism region, whereas the greater difference in genotypes' reproductive potentials, the wider polymorphism region. The complex effect of maternal selection and overlapping generations happened to be as follows [7]: overlapping

generations always tend to dilate the polymorphism region, odd and even external cycles produce various types of polymorphism regions. Particularly, odd external cycles expand but only slightly the coexistence region at low survival of reproductive individuals; with increasing survival of reproductive individuals, this region expands together with gradual decreasing extension of the region due to maternal selection. On the contrary, even cycles produce the greatest extension of the polymorphism region at low survival of reproductive individuals, at that, with large difference in reproductive potential of genotypes maternal selection dilates the region of alleles' coexistence, but classic selection becomes more effective in maintaining polymorphism with low values of this parameter.

Conclusion: Maternal selection [2] and overlapping generations [8] can facilitate the stable coexistence of alleles under temporally fluctuating environment. Using mathematical models, we considered the complex effect of these two factors on the maintenance of genetic polymorphism in cyclically changing environments. We focused on asymmetric cyclic selection, which allows us to describe fluctuations of environments similar to food resources cycles with rare peaks and prolonged decline of prey abundance. Such environment provides conditions for r-K selection, at which 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) [9, 10]. With the asymmetric external cycle, dominant genotypes that produce more offspring most often concede to recessive genotypes with low reproductive potential to be able to adapt to limited food resources. One can observe similar situation in arctic foxes we focused on in our models. The obtained results showed that compared with the simple Mendelian inheritance in the classic model, maternal selection and overlapping generations increases the chances of maintaining polymorphism in populations of arctic foxes.

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