

NEWS AND COMMENTARY

Cyclic fitness variation and polymorphism

Cycling selection for litter size in arctic foxes

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Various evolutionary scenarios have been suggested to explain the regular numerical cycles in some microtine rodents (Nespolo, 2007). The numbers of arctic foxes in inland populations also have approximately 4-year cycles in response to the cycles in numbers of small rodents, mainly voles and lemmings. Using a detailed pedigree of captive animals, Axenovich *et al.* (2007) concluded that the variation in arctic fox number was mainly the result of variation in litter size determined primarily by polymorphism at a major gene. To explain the maintenance of this polymorphism, they presented a model in which the recessive genotype had the highest litter size in bad years and the lowest litter size in good years (Table 1a). In their model, 'In years with low food supply, the survival rate of the small litters produced by A_2A_2 mothers was assumed to be k -times higher than that of large litters produced by A_1A_1 and A_1A_2 mothers.'

These litter sizes can be given as standardized relative fitnesses as in Table 1b. The conditions for genetic polymorphism for this model were first given by Haldane and Jayakar (1963) in which they showed that a polymorphism was maintained when the arithmetic mean fitness of genotype A_2A_2 over generations is greater than 1 and the geometric mean fitness of A_2A_2 is less than 1. To meet these conditions, assuming that there are 3 bad years to every good year (Axenovich *et al.*, 2007), then $1.666 < k < 1.718$, a range of 0.052, which encompasses the $k = 1.7$ value given as a stable polymorphism example by Axenovich *et al.* (2007). Or, for a stable polymorphism with standardized fitnesses, $1.111 < k' < 1.145$, a range of only about 3%. In other words, the conditions for polymorphism maintenance with dominance and cyclic fitness variation are quite restrictive (Hedrick *et al.*, 1976).

Further, Axenovich *et al.* (2007) concluded that the 'male effect was negligible' at this gene, indicating that selection is occurring only in females and not in males. Female-only selection can be modeled using the standardized fitnesses given in Table 1c. In this case, the conditions for a stable polymorphism, $1.056 < k'' < 1.063$, are even more restrictive, encompassing a range of less than 0.7%. In other words, it appears unlikely that litter sizes and subsequent survival of the pups are so finely balanced that they meet these very limited conditions for a balanced polymorphism under cycling selection.

It is possible that other types of balancing selection with broader conditions for stable polymorphism, such as differential selection at different locations or genotype-specific habitat selection (Hedrick, 1986, 2006), or some kind of frequency-dependent selection, may also be acting so that the conditions for stability are less restrictive. Or, as suggested by Axenovich *et al.* (2007), the

farmed foxes analyzed for litter size may have inherited the allele for small litter size from coastal populations, which have small litters and reproduce every year, and the allele for large litter size from inland populations, which have large litter sizes but do not reproduce every year. If this putative litter size gene can be located and the different alleles characterized molecularly, perhaps the type of balancing selection, or other explanations, can be identified. These concerns do not detract from the fascinating statistical conclusion of Axenovich *et al.* (2007) that the best genetic model to explain the observed bimodal litter size in arctic foxes is one with a single major gene.

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Editor's suggested reading

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van Oosterhout C, Joyce DA, Cummings SM (2006). Evolution of MHC class IIB in the genome of wild and ornamental guppies, *Poecilia reticulata*. *Heredity* 97: 111–118; advance online publication, 31 May 2006 (doi:10.1038/sj.hdy.6800843).

Table 1 (a) Litter size and (b) standardized fitnesses for different genotypes for arctic foxes in good and bad years and (c) standardized fitnesses for female-only selection

Environment	Genotype		
	A_1A_1	A_1A_2	A_2A_2
<i>(a) Litter size</i>			
Good	12	12	8
Bad	12	12	$8k$
<i>(b) Standardized</i>			
Good	1	1	0.6667
Bad	1	1	$0.6667k'$
<i>(c) Standardized with female-only selection</i>			
Good	1	1	0.8333
Bad	1	1	$0.8333k''$