

NEWS AND COMMENTARY

A simple adaption to cycling selection

A complex population dynamic explained by a single-locus Mendelian model for litter size

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It is well recognized that some of the most sophisticated areas in biology in terms of theory-based research are population ecology and life history quantitative genetics (Weber, 2000). Whereas the former has been successful in identifying the endogenous and exogenous factors that predict population cycles, the latter has become the standard framework for predicting the phenotypic optima that a population could attain by adaptive evolution. Surprisingly, however, there have been few attempts to link both approaches in a general and mechanistic model of life – history based population dynamics. Probably the central question needed to be solved first, as Saccheri and Hanski (2006) posed it, is ‘To what extents, and under which circumstances, are population dynamics influenced by natural selection?’ For the case of the arctic fox, Axenovich *et al.* (2007) gave a potential answer. Litter size is a major life history trait in mammals, and hence a component of fitness. Coastal populations of the arctic fox depend on stable food resources (sea birds, fish, seals and marine invertebrates) and produce litters of moderate size. Conversely, inland populations feed on small rodents and exhibit cycling population fluctuations. Unlike most other mammals, litter size of the arctic fox presents a bimodal pattern of small (about eight pups) and large (about fourteen pups) litters.

By using a non-standard quantitative genetic approach (complex segregation analysis), Axenovich *et al.* (2007) took advantage of a long-term record of breeding obtained from farmed foxes to show elegantly, a striking mode of inheritance of litter size in this species. They found that litter size in the arctic fox is determined by a classic Mendelian model with recessive control of low litter size. Using this result, Axenovich *et al.* (2007) proposed a model of balanced polymorphisms that predicts the population dynamics of the inland and coastal fox populations.

According to Axenovich *et al.* (2007), the population cycles in the inland population can be the consequences of fluctuating soft selection (i.e., dependent on either density or genotype frequencies in the population) acting on litter size. Food availability affects the survival rate of young, but not litter size at birth. Compared with small litters, pups in large litters experience

disproportionately higher mortality when food is scarce. This trend represents a selective advantage for small litters in bad years. When this happens, the recessive allele increases its frequency in the population producing more mothers that give birth to small litters (Figure 1a). During good years (every 4 years) however, individual survival in small and large litters are similar, and the dominant allele increases its frequency in the population (Figure 1b). Axenovich *et al.* (2007) showed that the recessive allele would be fixed in a few hundreds of generations if survival of small litters is at least 1.5 times higher than in large litters, which would have been the case for the coastal population (which does not experience cycles). However, in the inland population this genetic polymorphism is maintained since gene frequencies fluctuates greatly between good and bad periods (Figure 1b).

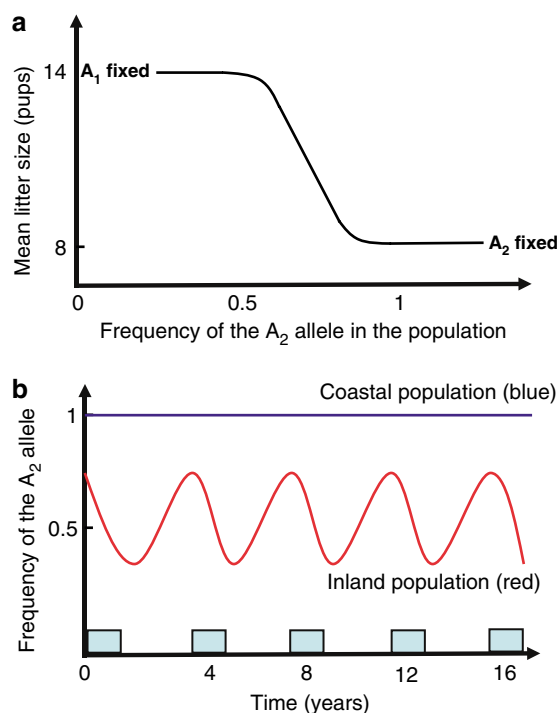


Figure 1 Potential selection-based mechanism of population cycles in the arctic fox. Small litters are produced by the recessive homozygous (A_2A_2) genotypes and large litters are generated by the dominant A_1 allele in this single-locus diallel model with dominance (a). In the coastal population, where food availability is stable over time, the A_2 allele is fixed: all mothers are A_2A_2 and produce small litters and no population cycles are described (b, blue line). However, in the inland population, drastic food increases occur every 4 years (bars) in the form of rodent outbreaks. During these periods, the survival rate of small litters produced by A_2A_2 mothers is equal to the survival of large litters (produced by either A_1A_2 or A_1A_1 mothers). During periods of low food availability (between bars), however, survival rate of small litters is k -times higher than in large litters. According to the simulations of Axenovich *et al.* (2007), the maintenance of this genetic polymorphism in the inland population over several hundreds of generations occurs with a k value of about 1.7. This means that soft selection (i.e., selection dependent on genotype frequencies) is responsible for the population cycles that inland populations of the arctic fox experience.

The first attempt to link demographic patterns with life history evolutionary dynamics was Chitty (1952), who proposed that the population cycles of microtine rodents depended on natural selection operating on the genetic composition of population life histories. Implicit in this explanation was the existence of fluctuating additive genetic variance in life history traits. Three decades after this, Boonstra and Boag (1987) tried to test this hypothesis by a standard quantitative genetic experiment which failed to demonstrate enough genetic variation in life histories, and hence to support the Chitty hypothesis. If Axenovich *et al.* (2007) relied only on the polygenic part of their model (i.e. traits determined by many genes of small effects; the basis of classic quantitative genetics), the conclusions would have been the same as Boonstra and Boag (1987) since heritability of litter size in arctic foxes was very low. However, the novel use of complex segregation analysis that Axenovich *et al.* (2007) applied, made the difference. This major gene effect gives a special importance to non-additive genetic variance, especially dominance variance, something that standard quantitative genetic models do not consider. Given that a great deal of the theory of Life History Evolution has been constructed under the polygenic assumption of gene effects (many books have been published on this grounds: Stearns, 1992;

Mousseau *et al.*, 2000; Roff, 2002), the paper of Axenovich *et al.* (2007) could shake the very roots of the Life History paradigm.

Natural selection can influence population dynamics in various circumstances, but in most cases acting on life histories. Recent studies addressing the link between life histories and population dynamics have shown that natural selection can promote population cycles. Either by soft selection, as in the Axenovich *et al.* (2007) study (lizards: Sinervo *et al.*, 2000) mediated by predator-prey dynamics that increase variation in life histories (algae: Yoshida *et al.*, 2003), or even by hard selection in physiological traits that affect dispersal ability (insects: Haag *et al.*, 2005). The contribution by Axenovich *et al.* (2007) has the value of providing a nice textbook example of a major life history trait explained by the simplest known genetics: the single locus model of Mendel peas.

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Axenovich TI, Zorkolsteva IV, Akberdin IR, Beketov SV, Kashtanov SN, Zakharov A *et al.* (2007). Inheritance of litter size at birth in farmed arctic foxes (*Alopex lagopus*, Canidae, Carnivora). *Heredity* **98**: 99–105.

Boonstra R, Boag PT (1987). A test of the chitty hypothesis: inheritance of life-history traits in meadow voles *Microtus pennsylvanicus*. *Evolution* **41**: 929–947.

Chitty D (1952). Mortality among voles (*Microtus agrestis*) at Lake Vyrnwy, Montgomeryshire, in 1936–1939. *Phil Trans R Soc Lond B* **263B**: 505–552.

Haag CR, Saastamoinen M, Marden JH, Hanski I (2005). A candidate locus for variation in dispersal rate in a butterfly metapopulation. *Proc R Soc B* **272**: 2449–2456.

Mousseau TA, Sinervo B, Endler J (2000). *Adaptive Genetic Variation in the Wild*, 1st edn. Oxford University Press: New York. p 265.

Roff DA (2002). *Life History Evolution*. Sinauer Associates Inc.: Sunderland, MA, USA.

Saccheri I, Hanski I (2006). Natural selection and population dynamics. *Trends Ecol Evolut* **21**: 341–342.

Sinervo B, Svensson E, Comendant T (2000). Density cycles and an offspring quantity and quality game driven by natural selection. *Nature* **406**: 985–988.

Stearns SC (1992). *The Evolution of Life Histories*, 1st edn. Oxford University Press: Oxford. p 249.

Weber TP (2000). Biological objects, units of selection and character decomposition. *Trends Ecol Evolut* **15**: 304–305.

Yoshida T, Jones LE, Ellner SP, Fussman GF, Hairston NG (2003). Rapid evolution drives ecological dynamics in a predator-prey system. *Nature* **424**: 303–306.

Editor's suggested reading

Charbonnel N, Pemberton J (2005). A long-term genetic survey of an ungulate population reveals balancing selection acting on MHC through spatial and temporal fluctuations in selection. *Heredity* **95**: 377–388.

Tomruk J, Niklasson M, Parker ED (2004). Maintenance of clonal diversity in *Dipsa bifurcata* (Fallen, 1810) (Diptera: Lonchopteridae). II. Diapause stabilizes clonal coexistence. *Heredity* **93**: 72–77.

Vuorinen JA, Eskelinen O (2005). Long-term stability of allozyme frequencies in a wood lemming, *Myopus schisticolor*, population with a biased sex ratio and density fluctuations. *Heredity* **94**: 443–447.