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NEWS AND VIEWS

PERSPECTIVE

The challenge of demonstrating contemporary natural selection on polygenic quantitative traits in the wild

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In a *From the Cover* article in this issue of *Molecular Ecology*, Ashraf et al. (2022) apply genomic prediction methods, devised by breeders to inform artificial selection, to understand the genetic component of variation in highly polygenic quantitative traits in Soay sheep (Figure 1). These methods have allowed them to investigate the effects of contemporary natural selection on genetic variation underlying these traits in the wild (Hunter et al., 2022). Genomic prediction approaches promise to enhance our understanding of the evolution of highly polygenic quantitative traits in the wild and may allow us to document concrete examples of their natural selection in real time in systems that would otherwise be intractable.

To appreciate the broader significance of this research, we should bear in mind that scenarios of natural selection acting upon quantitative traits of charismatic megafauna in the wild occur frequently in popular descriptions of evolution. In *The Origin of Species*, Charles Darwin imagined “the swiftest and slimmest wolves” being naturally selected when only “the fleetest prey” were available (Darwin, 1859 p. 90). More recently, in *Outgrowing God: A Beginner's Guide*, Richard Dawkins imagined a mutation causing “slightly longer claws” on a cheetah that “help it run just that little bit faster” and therefore have more surviving offspring (Dawkins, 2019 p. 179). These two examples (which are similar to many others found in textbooks and popular literature) are purely hypothetical. We do not currently have direct field evidence for a change in allele frequencies driven by natural selection to back them up.

In the absence of direct evidence, Darwin, Dawkins and many others have built a case based on an analogy to artificial selection, nested within a wider argument for the logic of the Darwinian mechanism. Darwin compared his wolf to a greyhound and Dawkins compared his cheetah to, inter alia, a whippet, a Shetland pony and a Brussels sprout. These arguments and analogies may be intuitively pleasing and so convincing as to seem obviously true. But the analogy to artificial selection has limitations, as I describe below.

The circumstances under which selection can change a quantitative trait are more stringent than is perhaps immediately apparent. One helpful way to think about this, devised in the context of artificial selection, is the breeder's equation (Lush, 1937). This states that change in a trait's mean value in a population is proportional to both the strength of selection and the trait's heritability. Heritability is the proportion of variation in a trait that is due to additive genetic effects and it can be increased by reducing environmental variability and increasing genetic diversity. Breeders exert strong selective pressures for single traits that they can measure precisely generation upon generation. But selection is not all that they do. They also work hard to increase trait heritability by introducing new genetic variation from carefully chosen individuals and by providing uniform environmental conditions. Their environmental manipulations can also break trade-offs between traits.

Take, for example, Darwin's comparison between a wolf and a greyhound. In the wild, a wolf cannot just be swift and slim. As Darwin noted, it must also have strength to “master its prey” (Darwin, 1859, p. 90), so there are trade-offs among its traits. There are also “various causes of destruction” in the wild, many of which are greatly affected by chance, as Darwin added in an extended discussion of his wolf analogy in the 1869 edition of *The Origin of Species* (Darwin,

FIGURE 1 Part of a natural population of Soay sheep in the Village Bay study area on the island of Hirta, St Kilda (Scotland). Photo: Martin Stoeffel (University of Edinburgh)

1869, p. 104). These stochastic deaths reduce the efficacy of natural selection. We could also note that environmental variability in the wild may cause selection differentials to fluctuate and heritability of traits to be reduced. Gene flow from populations in areas with slower prey may counteract selection for speed.

In contrast, greyhound breeders can break trade-offs. By providing processed food they remove the need for dogs to master their prey. By providing safe conditions they minimize chance causes of death. By providing uniform environments they maximize heritability. They select on the basis of precise measurements of the running speed of adult dogs on a flat running track, and apply these selective pressures generation upon generation. They prevent their dogs from breeding with slower dogs, and encourage them to breed with faster dogs. They sometimes introduce new genetic variation that may be disadvantageous in the short term, but beneficial after several generations.

The purposeful activities of the breeder mean that artificial selection is not just analogous to natural selection. It may also be likened to intelligent design, the position that Darwin and Dawkins are arguing against. A greyhound is engineered from animate materials, somewhat as a watch is engineered from inanimate materials. Artificial selection has an artificer. This limits its value as evidence for the efficacy of natural selection. Given the limitations of the analogy to artificial selection, it is highly desirable in making the case for the efficacy of natural selection on quantitative traits to have direct evidence.

How could we gain direct evidence for the action of natural selection upon the speed at which wolves or cheetahs can run? This would not be a trivial undertaking, as experience with other study systems shows us. Whilst very many examples of phenotypic changes under environmental change in the wild have been documented (Sanderson et al., 2022), it is much harder to demonstrate the genetic basis of these changes. To do so ideally requires long-term analyses of pedigrees of phenotyped individuals in the wild, or studies of families or clones in uniform environments accompanying studies of populations in the wild. Both approaches require great effort, and the uniform environment approach is especially difficult for megafauna. When Sanderson et al. (2022) compiled 7338 estimates of phenotypic change in wild populations, for only 24% of these had a genetic component to the change been shown. They noted that “precise attribution to genetic versus plastic change is exceptionally difficult” (Sanderson et al., 2022, p. 1032). Of their 7338 examples, only 37 were for mammals, contained in one study on rabbits, one on snow voles and one on red squirrels.

When long-term studies of pedigreed populations of birds and mammals have been done, evidence for change in the heritable component of particular traits has been hard to come by. As noted by Merilä et al. in 2001, “there are remarkably few cases where direct observations of natural populations have revealed microevolutionary changes occurring, despite the frequent demonstration of additive genetic variation and strong directional selection for particular traits” (Merilä et al., 2001 p. 199). This is not what the breeder's equation would predict, so, “explaining this mismatch between natural world observations and theoretical expectations—which work under controlled conditions—has been a major motivation for much of the recent work on the quantitative genetics of wild populations” (Charmantier et al., 2014 p. 8). The difficulty of identifying natural selection acting on the genetic basis of particular animal traits has persisted (but for some positive examples see: Bonnet et al., 2017; Evans & Gustafsson, 2017; Pigeon et al., 2016), leading quantitative geneticists working on wild animals to seek evidence for natural selection on fitness itself rather than particular traits underlying fitness (Bonnet et al., 2022).

High-throughput, inexpensive, DNA sequencing means that today it is possible to cut through some of the difficulties of partitioning phenotypic variation between environmental and genetic effects, and directly characterize evolution in natural populations at the nucleotide level. This is particularly feasible for traits governed by one or a few loci of large effect, giving us examples of natural selection for such traits in animals in the wild (e.g., Lai et al., 2019; Linnen et al., 2009). However, as Fisher (1930) realized, quantitative traits like wolf and cheetah speed are likely to be highly polygenic, so adaptive changes will involve allele frequency changes at very many loci, and any new mutation will be just one of many causes of variation (Barton, 2022; Fisher, 1930). This makes the direct characterization of allelic changes underlying such traits difficult. New methods are needed to make this possible.

Since genome-wide genotyping has become available at scale, breeders have developed genomic prediction methods. These have enabled them to impose stronger selective pressures than ever before, leading to new gains in desirable traits, especially in traits with low heritability (García-Ruiz et al., 2016). Taking genome-wide allele frequencies and phenotypic measurements in a large training population, genomic prediction uses regression models to predict an effect size for each locus. These effect sizes can then be used to assign a genomic estimated breeding value (GEBV) to other genotyped individuals, summarizing their genetic merit for a trait of interest. This allows breeders to, in effect, bypass phenotypes and select directly on genotypes. The success of these methods even on traits that have previously been subject to considerable breeding effort highlights how weak phenotypic selection can be for quantitative traits even under controlled conditions. In genomic prediction, the exact mechanisms by which the vast majority of the loci affect the trait of interest are unknown, but this knowledge is not necessary for the method to work.

Genomic prediction is therefore a promising method to allow evolutionary biologists to cut through the noise of environmental effects in natural populations, and directly examine what is happening at the genomic level for polygenic traits. Ashraf et al. (2022) have done this in the current issue of *Molecular Ecology* for Soay sheep, testing the effectiveness of different genomic prediction models on their data. Using ~36,000 SNPs genotyped in around 1200 sheep phenotyped for polygenic quantitative traits, they find that genomic prediction works well with models that allow some loci to have zero effects and others to have large effects. For example, they gained accuracies of up to 0.64 for bodyweight, where accuracy is the mean correlation between GEBV and bodyweight adjusted for nongenetic effects (due to sex, age, birth year, capture year and animal identity), scaled by the square root of the heritability. This suggests that they are capturing a large proportion of the genetic component of bodyweight in the population.

To be clear, their results do not mean that they can predict the actual bodyweight of any particular individual with great accuracy. They estimate narrow-sense heritability of bodyweight to be 0.36 even after the bodyweight measurements have been adjusted for the effects of sex, age, birth year, capture year and animal identity. Thus, only a small proportion of variance in bodyweight in the population is due to genetic effects. The success of Ashraf et al. (2022) is that they can predict these small genetic effects with some accuracy.

These methods equip the research group to examine whether or not the bodyweight of the Soay sheep population is under selection in the wild. In Hunter et al. (2022) they apply genomic prediction to many generations of the sheep sampled over a 35 year period. They compare trends in mean GEBVs for bodyweight with trends in actual bodyweight (adjusted for age and sex). Paradoxically, they find GEBVs increase but actual weights to decrease in their population over time. They interpret this as cryptic microevolution, arguing that the population has responded to natural selection for higher bodyweight at the genomic level but environmental or demographic conditions have caused lower bodyweight at the phenotypic level.

While this slightly baffling situation is unlikely to replace easier-to-understand hypothetical examples of natural selection on wild animal quantitative traits in the popular literature, it represents a significant advance for the field. By pioneering genomic prediction methods in the exceptionally well-studied Soay sheep population, this work opens up the way for more widespread searches for natural selection acting upon quantitative traits in other wild populations (for an example in trees see Metheringham et al., 2022). Perhaps one day this will extend to the genomic basis of speed in wolves and cheetahs. Meanwhile, the results remind us that the wild is a complicated place; far more complicated than a breeder's paddock.

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DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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