Research Paper

Improving the efficacy of selection on complex traits—A brief review of quantitative genetic methods and considerations for measurement of phenotypes

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ABSTRACT

Many behavioral traits appear to be complex, with an assumed distribution in genetic liability underlying known and unknown environmental influences. Quantitative genetic methods enable more effective selection on single or multiple complex traits than selection on phenotypes because of the estimation of additive genetic variance in the population (the chief cause of resemblance of relatives and the only genetic component that can be estimated from observations on the population) and estimated breeding values of individuals. Estimation of genetic correlations between multiple traits reveals the effects selection on 1 trait will have on the breeding values of others and inform of unfavorable genetic relationships between objective traits. Improvement in multiple traits can be optimized via the use of selection indices, making the best use of all phenotypic information available to achieve specific selection objectives. Therefore, quantitative methods offer effective means of improving the accuracy of selection of behavioral traits. Quantitative genetic methods use phenotypic data on a large and representative proportion of the population, which have in livestock species typically taken the form of empirical measurement of continuous variables. Obtaining behavioral phenotypes presents challenges inherent in quantifying behaviors, but certain steps can be taken in the design of phenotypic protocols to ensure that phenotypic data are conducive to quantitative genetic analysis.

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Introduction

The recent conference in Canine Behaviour and Genetics took place in London, England, on June 27 and 28, 2015, with the aim of bringing together stakeholders with an interest in improving behavior in working and pet dogs to facilitate discussions on future research into behavioral genetics. Speakers delivered talks on a range of topics, including empirical evaluation of physiologic influences on behavior, the challenges in defining phenotypes, and reporting the results of genetic analysis of behavioral traits. An implicit axiom common to all articles was that the existence of phenotypic variation means some individuals are more suited to certain tasks and that, provided genetic variation contributes to this phenotypic variation, selection can assist in improving the proportion of dogs potentially able to meet certain requirements. In this short communication, the quantitative genetic theory of complex traits will be reviewed with an emphasis on methods available to improve the accuracy, and therefore, the response of selection. The implications on protocols for obtaining phenotypic data required will be explored.

Eliciting change via selection

Selection is the only way to ensure a lasting and widespread improvement in an objective trait over generations. Although environmental factors are often hugely influential on individual performance, they must be rigorously applied to ensure consistent improvement, and environmental effects will always act against the backdrop of genetics.

Useful examples can be seen from livestock species. Average milk yield per cow per year in the United Kingdom has risen 46% in

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23 years from 5,151 liters in 1990 to 7,531 liters in 2013 (DEFRA, 2015). Although clearly improvements in environment, for example, and in nutrition will serve to enhance yields, genetic selection too has had a crucial role in improving performance. This example demonstrates the importance of both nature and nurture in achieving particular objectives. Selection improves the genetic background of the trait, and judicious management of particular environmental factors enables performance to approach biologic capacity for each individual. Comparison of the appearance of the domestic pig with its forebear, the wild boar, provides another example of the power of selection. No amount of environmental variation will account for the morphologic changes observed; if a neonatal wild boar piglet were placed with a litter of domestic pigs, it would not resemble its foster siblings at adulthood, implying different genetics is responsible for the distinct phenotypes.

Selection works by effecting unequal reproductive success across a phenotypic distribution of a particular trait, which is underpinned by genetic variation. In the case of artificial selection, this has often taken the form of a threshold (breed from the best). Accordingly, the mean genetic liability of the trait in the progeny generation is equal to the mean genetic liability of selected breeding parent animals. Thus, for the progeny generation, the distribution of genetic liability shifts in the direction of selection applied to breeding animals in the previous generation, with influences on the phenotypic distribution of the trait. Continued independent selection on different traits (e.g., size, shape, behavior) over multiple generations will result in the development of multiple lines of distinct appearance, often termed breeds (although the term breed may also have additional geographic and sociologic associations).

Phenotypic variation in the dog

The domestic dog, *Canis familiaris*, shows greater phenotypic variation in appearance and behavior than any other domestic species. The long period since domestication and intense selection applied to accomplish specialized and specific tasks has produced breeds as diverse in stature as the Great Dane and Chihuahua, in morphology as the pug and the dachshund, and in behavior as the border collie and the Anatolian shepherd dog. Comparison of the pug and dachshund is analogous to the example of the domestic pig and wild boar used previously; the morphologic differences are a result almost exclusively of selection. However, the comparison of the behavioral differences of the border collie and Anatolian sheepdog perhaps have more in common with the example of the dairy cow; there may be substantial environmental influences on behavior (e.g., training), but it is likely that there is some underlying genetic difference in propensity to herding and guarding behaviors.

Genetic architecture and parameters determining genetic improvement

Simple (Mendelian) versus complex traits

In some, often well-known, cases, all phenotypic variations are entirely because of allelic dominance at a single gene (known as simple or Mendelian traits). Diseases such as cystic fibrosis in humans and primary lens luxation and progressive retinal atrophy in some dog breeds are caused by a single mutant allele inherited in duplicate. Such disease-causing alleles are fortunately relatively easy to locate allowing the development of DNA tests. Importantly, DNA tests improve the accuracy of selection, enabling breeders to determine with absolute confidence the risk of producing affected offspring from 2 phenotypically unaffected parents at an age before the normal presentation of disease. For behavior, it may be possible to identify single genes responsible for very specific traits (e.g., pointing; Spady and Ostrander, 2008). However, the architecture of most traits is more complex because of the influence of both environmental and additive genetic variation.

Environmental variation

Complexity is introduced by the influence of environment on phenotypes. Multiple unique environmental influences overlay individual genetics, meaning that phenotypes are not perfect indicators of genetic liability. For example, beneficial genetics may be overlaid by poor environment and poor genetics by beneficial environment to both result in moderate phenotypes. Therefore, selection (which only acts on genetics) using phenotypes is prone to inaccuracy, with a concomitant effect on the response observed. Variation because of environment is particularly important in canine behavior where training may play a large role in determining phenotype—are the dogs with the most desirable phenotypes those with the greatest genetic propensity or simply those subject to the most effective training?

Additive genetic variation and breeding value

Complexity is also introduced at the genetic level by traits being influenced by multiple genes and allelic additivity (any departure from complete dominance where the heterozygote is phenotypically identical to the dominant homozygote). Thus, rather than binary phenotypes being underpinned by 3 distinct genotypes as with Mendelian recessive traits, phenotypes of complex traits (e.g., bodyweight, livestock production traits, and some behaviors) are underpinned by a near continuous distribution of genetic liability and tend to display continuous variation (in part because of the influence of environmental variation as discussed). However, the presence of genetic variation means that these traits will respond to selection.

Additive genetic variation is also the principle cause of the resemblance of relatives (Falconer and Mackay, 1996). Despite the name, the presence of additive genetic variance carries no implicit assumption of additive gene action. Rather it is the variance of the cumulative average effects of individuals' genes (and is therefore dependent on genotypic values and gene frequencies in the population). The average effects of individuals are indeterminable, but they do determine the mean genotypic value of any progeny. Therefore, progeny phenotypes can be used to judge the genetic or breeding value of an individual, and the breeding value of an individual is twice the mean deviation of progeny performance from the population mean (Falconer and Mackay, 1996). Because it is the primary source of resemblance between relatives, the additive genetic variance is the only genetic variance component that can be estimated from phenotypic observations on the population (Falconer and Mackay, 1996), the degree of relationship between individuals with phenotypic data being provided by pedigree data.

Heritability

The proportion of phenotypic variance attributable to additive genetic variance is the *heritability* of a trait in a particular population (Falconer and Mackay, 1996). Thus, the heritability describes the reliability of phenotypes as a guide to underlying genetics (breeding values) and informs of the likely success of selection in improving phenotypes. A high heritability (approaching 1) indicates that phenotypes are very good indicators of breeding values, the environmental variance is small, and the response to phenotypic selection will be large. Conversely, a low heritability (approaching 0) means that additive genetic variation makes only a