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NEWS AND COMMENTARY

Genetics of social behaviour

Genetic influences on social dominance: cow wars

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If you happen to be travelling through the Valle d'Aosta in Italy, near Switzerland, no doubt you will want do so at a time you can view the 'Battailes de Reines' or the Battle of the Queens. Cows (the queens) are pitted against each other in tournaments involving bloodless fights. Apparently winning cows can elicit submission with just a glance. For centuries, tournaments have been held to determine which cow is most dominant and these are highly organized, ritualized and structured battles, with deep records of wins, losses and bloodlines held by the local farmer's association. Such data are perfect for evaluating the genetic influences on social dominance using modern quantitative genetic analyses based on pedigree data. What, then, determines which cow will be the likely winner of the Battailes de Reines? Can breeding lead to socially dominant queens that rule all others and therefore the Batailes de Reines? Sartori and Mantovani (2013) address this issue by examining genetic effects on social dominance in cattle that have participated in this century-old tradition. Of course, studying what makes a cow dominant is, by itself, clearly worthwhile. However, examining genetic influences on social dominance illustrates some of the complexities of explaining how inheritance influences behaviour.

Social dominance presents special challenges because it is hard to define in a way that lends itself to measurement as a trait of an individual. In fact, the genetic influences of social dominance have a long history of eliciting controversy because, by definition, at least two individuals have to be present for the trait to be expressed. How then, do genes that are expressed within an individual contribute to a trait that requires two individuals for expression? There are many such behavioural traits, for example, courtship, mate choice, aggression, social learning and communication, all of which require at least a pair of individuals be present to be expressed. It has long been recognized that such traits presents special problems for studying genetic influences on behaviour. As Manning (1961, p 84) wrote in his classic study of the genetics of mating speed in *Drosophila*: 'There is perhaps little reality in the heritability of a character which involves the interaction between two individuals'. Of course, he did go on to measure the realized heritability from selection lines, but he knew the speed with which courtship proceeds to mating depends on both of the individuals that are interacting and so he assigned courtship to the pair. Genetically, this is obviously not biologically realistic.

We now study a phenotype expressed in an interaction by recognizing that each interactant acts as an environment for the other individual. This is accomplished by including a consideration of 'indirect genetic effects' or IGEs. The theory underlying IGEs follows a generalization of maternal genetic effects models (Griffing, 1967; Moore *et al*., 1997). In brief, the trait of an individual that requires a social interaction to be expressed reflects both the genes of the focal individual (the direct additive genetic influences) and the genes of the social partner (the indirect genetic influences), much like traits of offspring reflect genetic differences in maternal environments as well as direct genetic influences in the offspring. Sartori and Mantovani put it well: 'an individual providing the direct information 'good at winning' also carries the information 'bad at losing' as an indirect effect.' Because there must be both winners and losers in the population, the prediction is that there will be a genetic correlation of -1 between direct and indirect genetic effects. If such a complete genetic trade-off exists, there should be no change in the population mean even with genetic variation underlying both direct and indirect components of social dominance.

Sartori and Mantovani make use the records of cows that have participated in the Batailles de Reines from 2001 to 2011. The regional farmers' association maintains detailed records, and the authors use them to calculate influences and inheritance affecting the dominance status of the subjects. Using records on 8159 cows in a pedigree containing 17 579 individuals, they modelled four partitionings of phenotypic and genetic variance: (1) random environment and direct genetic effects; (2) random environment, associative (social) environment and direct genetic effects; (3) random environment, direct genetic effects and indirect genetic effects; (4) the full model with both random and social environments, and direct and indirect genetic effects. Models with direct and indirect genetic effects also included the covariance between the two. In models that ignored IGEs, heritability was low. In models with direct and indirect genetic effects, direct and indirect effects were similar in magnitude. Direct heritability and indirect (IGE) heritability were moderate, but total heritability was again low. This is because the genetic correlation between direct and indirect genetic effects was, as predicted, effectively -1.

The implications are that despite standing genetic variation, social dominance does not appear to change in the population. Given the time series of the data, Sartori and Manovani could examine how the direct, indirect and total breeding values changed over time. Even though the contributions of direct and indirect breeding values both

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increase, the total breeding value remained consistently low because of the negative covariance between the two. Selection on an increased likelihood of winning resulted in an equal change in how to lose and no change in the mean trait over time. This is as predicted by theory and previous studies in red deer (*Cervus elaphus*; Wilson *et al*., 2011) and cockroach (*Nauphoeta cinerea*; Moore *et al.* 2002). Selecting for good winners produces equally good losers in the presence of these winners. Despite evolution, the mean social dominance does not change because there has to be a winner for every loser. For the famers who compete their cows, the only solution is to encourage other communities to hold competitions in other populations—as the cockroach study showed, response to selection for good winners may become apparent if matched with individuals from another population that has a different selection history.

The age-old 'nature versus nurture' arguments persist partly because those who study behaviour from a psychological or ecological perspective have difficulty reconciling the flexibility of behaviour with genetics. This view, however, neglects the fact that nothing develops in a genetic vacuum or without environmental influences. Moreover, nothing evolves unless the variation among individuals reflects genetic influences. Incorporating an IGE perspective, which acknowledges the important role of social environments that both create selection and can themselves evolve, provides a context where both genetic and environmental influences contribute to the differences we see among individuals. Social dominance is a classic case where environmental influences, including social environments, will be critical in determining how individuals behave. Nevertheless, as this study of social dominance in cows illustrates, genetic make-up can have a significant role.

CONFLICT OF INTEREST

The author declares no conflict of interest.

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