Competitive Vs. Classical Model To Evaluate The Genetics Of Fighting Ability In Valdostana Cattle

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Introduction

Behaviour is one of the most complex phenotypes studied because of the strong influence that the environmental and non additive genetic components exert. In the classical quantitative genetic model only a direct additive genetic component is taken into account. However, there are many traits which expression depends, at least in part, by interactions with conspecifics: such as the "Interacting Phenotypes" (Moore et al. (1997)). All these traits are mainly social behaviours, as courtship or social dominance (Meffert et al. (2002); Bleakley and Brodie (2009)), but they can also be productive traits affected by social contest, as the daily gain of species managed in large groups (Arango et al. (2005); Van Vleck et al. (2007)). In particular, interacting phenotypes are simultaneously environments and evolving traits, because they can be at the same time the environment for a focal individual and the trait under selection for a conspecific interacting with it. Thus, they are environments changing in response to selection, and genetic models accounting for them need to be expanded with social effects (Bergsma et al. (2008)), i.e., including both a classical additive component and an indirect genetic effect (IGE; Wolf et al. (1998)) due to the interaction between individuals and the group. In previous studies (Mantovani et al., (2007); Sartori and Mantovani (2009)), we investigated the direct genetic effect of the fighting ability in cows by analysing traditional fighting tournaments in the Valdostana breed. The aim of the present study is to compare the classical approach for estimating genetic fighting ability with two other methods that assess directly (at a phenotypic level) or through a competitive model the fighting ability in Valdostana cows.

Material and methods

Experimental settings. Data on Fighting ability has been collected from yearly battle contest rankings obtained by participant Valdostana breed cows (i.e., *Batailles de Reines*), in the Aosta Valley region (northern-west Alps, Italy). Battles consist in 20 preliminary tournaments over a year's time and a final match which is disputed by the best qualified at the end of the season (Mantovani et al, (2007)). Participants duel in knock-out bloodless matches contending a heap of earth (Sartori and Mantovani (2009)). These traditional competitions existed for centuries and are not cruel for animals (Mantovani et al. (2007)). Tournaments vary in size (16-153 participants) and they consist in contemporary battle boards divided in three weight categories in which cows faceoff one on one. The looser is eliminated and the winner moves on to engage another fight at a superior level. Winners of

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the final tournament achieve the title of "Queen" of the year. The best results from 6 years of fights (9769 records) disputed by 5236 cows were used. As in a previous study (Sartori and Mantovani (2009)), the rank of the participants was scored with a "Placement Score" (PS) computed as $PS_{ijl}=k+T_i+d_j+2w_l$, with k=20 (starting value), T_i= weights of battles (i=0 for eliminatory and 7 for the final struggle), d_j=difficulty coefficient related to number of participants (j=-2,…,+2) and w_l=number of wins in the battle board (l=0,…, 8). Counter to PS, a "Competitive Placement Score" (CPS) was obtained by modifying the PS in a way to account for the opponent's strength. The CPS was obtained as follows: $CPS_{ijkm}=k+T_i+2d_j-2_b-(k-CPS_{ijka})$, where k=500 (starting value), i=0 for heats and 50 for final, d_j=the same as for PS, b=highest level of the battle achieved (b=0,…, 8) and CPS_{ijka}=last competitor's score.

Analysis. A single-trait genetic analysis was applied with a REML (Misztal (2008)) method comparing: i) a model based on a "Placement Score" (PS), related to the rank reached and the size of battle board (M1), ii) as M1 but using CPS, in order to account for the strength of the opponent in the phenotypic data (M2) and iii) a competitive model including the competitor effect directly as IGE and using the PS as the phenotype (M3). The latter model also takes into consideration the competitor's strength as IGE. After checking the non genetic fixed factors to be used in the model, the final linear model used in M1, M2 and M3 was the following:

$$y_{ijklmn}=\mu+YB_i*C_j+HY_k+AC_l+b_j*W_{m:j}+p_m+a_n(+\Sigma c_o)+e_{ijklmn}$$

where $y_{ijklmno}$ is the trait (PS in M1 and M3, CPS in M2), μ is the overall mean, YB_i*C_j is the effect of the yearly-battle i by weight category j (i=1,…,123, and j=1,…,3, respectively), HY_k is the Herd-Year effect (k=2337 levels), AC_l is the age class of the participant fighters (7 classes: ≤3, 4, 5, 6, 7, 8 and ≥9 years), b_j is the regression coefficient for each weight category j, $W_{m:j}$ is the individual covariate of weight within C_j, p_m is the random permanent environmental effect arising from the repeated data over the years of each individual (5236 levels), a_n is the random additive genetic effect (12476 levels, as animals in pedigree), Σc_o is the indirect genetic effect (accounted only in M3, 12476 levels) and e_{ijklmn} is the random residual term (~N(0, σ^2_e)). The assumptions about the structure of (co)variance were, in the most complete model, i.e. including IGE (M3), as follows:

$$\text{Var}\begin{bmatrix}\mathbf{a}\\ \mathbf{c}\\ \mathbf{p}\\ \mathbf{e}\end{bmatrix}=\begin{bmatrix}\mathbf{A}\otimes\sigma^2_{\boldsymbol{a}} & \mathbf{A}\otimes\sigma_{\boldsymbol{ac}} & \mathbf{0} & \mathbf{0}\\ \mathbf{A}\otimes\sigma_{\boldsymbol{ac}} & \mathbf{A}\otimes\sigma^2_{\boldsymbol{c}} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{I}\otimes\sigma^2_{\boldsymbol{p}} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{I}\otimes\sigma^2_{\boldsymbol{e}}\end{bmatrix}$$

where σ^2_a is the additive genetic variance, σ^2_c is associative genetic variance due to the competitor effect, σ_{ac} is the (co)variance between additive and associative components, σ^2_p is the permanent environmental variance, σ^2_e is the random residual variance, **A** is the numerator relationship matrix, **I** is an identity matrix, and ⊗ is the Kronecker product operator. Analysis were performed through a single-trait ENREML (Misztal (2008)). The competitive model applied (Arango et al. (2005)) was originally implemented by Muir and Schinckel (2002). The models were compared by using the Akaike Information Criterion (AIC, Akaike (1974)) based on the goodness of their fit. AIC is defined as the sum of the logarithm of the likelihood function reached at convergence with the number of independently adjusted parameters within the model.

Results and discussion

Variance components estimated for the three models are shown in Table1. Levels of h^2 were low but in accordance to the general low heritabilities of behavioural traits (Mosseau and Roff (1987)). Despite the small heritabilities, the different models have influenced the h^2 estimates: 0.090 for M1, 0.034 for M2 and 0.049 for M3, respectively. The values of AIC revealed M3 as the best method (AIC=17,119), and M2 as the worst (AIC=75,020; i.e., lower values reflect a better fitting).The insertion of competitor effect in M3 allowed us to obtain both direct and associative variance components, revealing the latter one as the main component of the overall h^2 (σ^2_c= 0.068 vs. σ^2_a=0.016). Total heritability, arising from the sum of both components came out to 0.049, i.e., which is lower compared to the estimates in M1 and M2, but in accordance with h^2 obtained by Plusquellec (2001) in the closely related study on the Swiss fighting breed Heréns. The associative component absorbs quotes of both the additive genetic and the permanent environmental variances (σ^2_p), as seen when comparing M3 with M1 (Table 1). Thus, individual performances are not only more a part of the environmental setting in which the behaviour takes place, but are also targets of selection. Moreover, considering the opponent in the model, the quote of residual variance proportionally shows a slight increase, as in M2 and M3. In M3 this mainly depends on the increment of total variability that the competitor assessment necessarily introduces.

Table1: Model fitting (AIC), trait considered (PS or CPS), variance components[α] and heritability estimates (h^2) from the different three models studied (M1, M2 and M3)

	AIC	Trait		Variance component				h^2	
Model:		PS	CPS	σ^2_p	σ^2_a	σ^2_c	Σ^2_r	Dir.	Ass.
M1	44437	√	-	1.106	0.702	-	5.971	0.090	-
M2	75020	-	√	86.0	19.0	-	461.0	0.033	-
M3	17119	√	-	0.012	0.016	0.068	1.601	0.009	0.040

[α]PS = placement score; CPS = competitive PS; σ^2_p = permanent environmental variance; σ^2_a = additive genetic variance; σ^2_c = associative genetic variance of competitors; σ^2_r = residual variance; h^2 Dir. = direct heritability; h^2 Ass.= associative heritability.

Fighting ability is a complex behaviour in which the environment exerts a strong influence and phenotypic expression largely depends on the genotype of the opponent (Wilson et al. (2009)). The few genetic evaluations of fighting performances in cattle (González Caicedo et al. (1994); Plusquellec (2001); Silva et al. (2006)) have shed light on a heritable component for this trait, but only a direct genetic component has been already estimated in this species. Thanks to the great amount of data coming from performances recorded in traditional cattle fights, the present study was able to consider opponent value and not just the individual in question. The direct inclusion of antagonist strength in the phenotypic data did not result in a successful model if we consider the fitting and h^2 estimates, due to the shift of part of the genetic variance to the residual (Table 1). However, our results indicate that the value of the opponent in fight studies could be better considered by directly introducing the competitor's effect as IGE in the model instead of using it in the score. Few studies have been carried out on associative genetic effects due to interacting phenotypes (Muir (2005), Arango et al. (2005), Van Vleck et al. (2007)), because the literature on IGEs is recent (Moore et al. (1997); Wolf et al. (1998)), as is the statistical package for analysis (Muir and Schinckel (2002)). IGEs in agonistic behaviours have been studied only in cockroaches (*Nauphoeta*

cinerea; Moore et al. (2002)), pigs (Lovendahl et al. (2005)) and deer mice (*Peromyscus maniculatus sonoriensis*; Wilson et al. (2009)), revealing a great importance in genetics.

Conclusions

This study corroborates the importance of associative components in investigating complex social traits, revealing fighting ability as a social behaviour that could be better analysed by considering the worth of the opponent in a contest. Moreover, worth is better taken into consideration in competitive models rather than in the phenotypic observation.

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