

# CURVILINEARITY IN THE RELATIONSHIP BETWEEN TRAITS COMPETING FOR RESOURCES: A GENETIC MODEL

J. Sölkner and J.W. James

Dept. of Livestock Sciences, Univ. of Agriculture, Gregor-Mendel-Str. 33, A-1180 Vienna, Austria  
 Dept. of Wool and Animal Science, Univ. of New South Wales, Kensington 2033, NSW, Australia

## SUMMARY

A genetic model is presented that is based on acquisition-allocation pleiotropy of loci coding for two traits competing for resources. If the acquisition of resources is limited (has a plateau), it is shown that such a model produces significant curvilinearity in the genetic relationship between the traits. The model will be used to check different methods of estimating curvilinear genetic relationships.

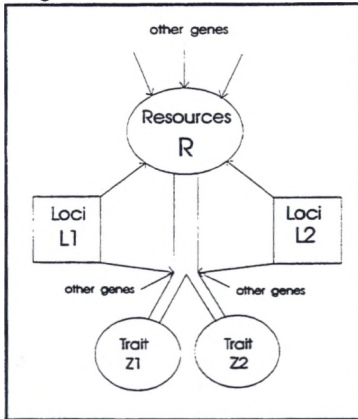
## INTRODUCTION

The population genetic concept of describing the relationship between traits using genetic and phenotypic covariance matrices relies implicitly on the assumption of linearity of such relationships. On the phenotypic level, though, the relationship between two traits is often found to be curvilinear and therefore can be described using polynomial regression equations. Whereas curvilinearity may sometimes be caused by scale effects, there is no reason to assume that relationships between traits are always linear on the genotypic level. Various physiological limitations and feedback mechanisms will potentially produce deviations from linearity.

One situation where one might expect curvilinearity is when two traits are competing for resources and resources are limited. In the present paper we examine a simple genetic model where two sets of loci are involved in the acquisition as well as in the allocation of resources. It will be shown that significant curvilinearity in the relationship between traits may be produced by such a model.

## THE MODEL

Figure 1: Graphical representation of the genetic model



We consider two traits,  $z_1$  and  $z_2$ , sharing the same pool of resources,  $R$  (Figure). The proportion of  $R$  allocated to  $z_1$  is  $P$ , so that

$$z_1 = PR \quad \text{and} \quad z_2 = (1-P)R \quad (1)$$

We assume that there are two sets of loci,  $L_1$  and  $L_2$ , each with a large number of genes with small effect. An increase of +alleles in  $L_1$  or  $L_2$  will have a positive effect on  $R$ , the resources acquired. An increase of +alleles in  $L_1$  will also effect an increase in  $P$ , shifting more resources toward  $z_1$ , whereas an increase of +alleles in  $L_2$  will have the opposite effect of increasing the share of resources available for  $z_2$ . Assuming that other genes also affect  $R$  and  $P$ , we may describe our model by

$$R = s + (1-s)F \quad \text{and} \quad P = t + (1-t)G \quad (2)$$

where  $s$  is the proportion of resources acquired independently of variation of +alleles in  $L_1$  and  $L_2$ , and  $t$  gives the proportion of resources allocated to  $z_1$  and  $z_2$  acting independently of  $L_1$  and  $L_2$ . The values of  $s$  and  $t$  will depend on effects due to loci belonging to the  $L_1$  and  $L_2$  complex but already fixed and to loci acting independently from  $L_1$  and  $L_2$ .  $F$  and  $G$  are functions of  $L_1^+$  and  $L_2^+$ , the

proportions of +alleles in the two sets of loci, describing the acquisition and allocation process due to  $L_1$  and  $L_2$ . One way of modelling F and G is to take

$$F = 1 - \exp(-k(L_1^* + L_2^*)/2) \quad \text{and} \quad G = \frac{L_1^*}{L_1^* + L_2^*} \quad (3)$$

F is a function that will asymptotically approach 1 as  $L_1^*$  and  $L_2^*$  increase. The shape of this function is determined by the parameter k. Function F introduces positive covariance between  $z_1$  and  $z_2$ , as with an increase in either  $L_1^*$  or  $L_2^*$  the total resources available for both traits increase. G, on the contrary, introduces negative covariance between  $z_1$  and  $z_2$  because as e.g.  $L_1^*$  increases, the share of resources available for  $z_2$  decreases.

Two essential features distinguish this model from earlier models by Rendel (1963, 1967, see also Sheridan and Barker, 1974) and by Houle (1991):

- the two sets of loci  $L_1$  and  $L_2$  exert some influence on the acquisition and on the allocation of resources (acquisition-allocation pleiotropy).
- the availability of resources does not increase linearly with the proportion of +alleles in  $L_1$  and  $L_2$  but approaches a limit.

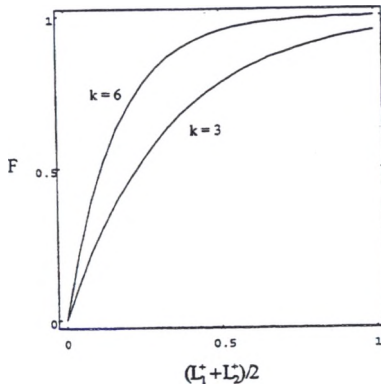
Whereas the second feature of the model is certainly a realistic one, the first is debatable. Houle (1991) used a model where acquisition and allocation of resources were determined by two independent sets of loci, arguing that while the assumption of no acquisition-allocation pleiotropy may not be realistic, it may be closer to reality that the converse assumption that all loci affect all characters. At least when we are concerned with energy input and output, as in many economically important traits in farm animals, it seems reasonable to assume that individuals ranking high for output will also be able to acquire more resources, i.e. eat more. The fact that not all the acquisition and allocation process is determined by the mechanisms assumed in F and G is dealt with by the inclusion of parameters s and t in formulae (2).

## RESULTS

The relationships between traits following the model described above were investigated by assuming a population where the average proportions of +alleles in  $L_1$  and  $L_2$  (denoted by  $L_1^*$  and  $L_2^*$ ) follow a bivariate normal distribution with means 0.5, standard deviations 0.1 and correlation 0. Simple quadratic regression between the standardized traits  $z_1$  and  $z_2$  was performed in both directions.

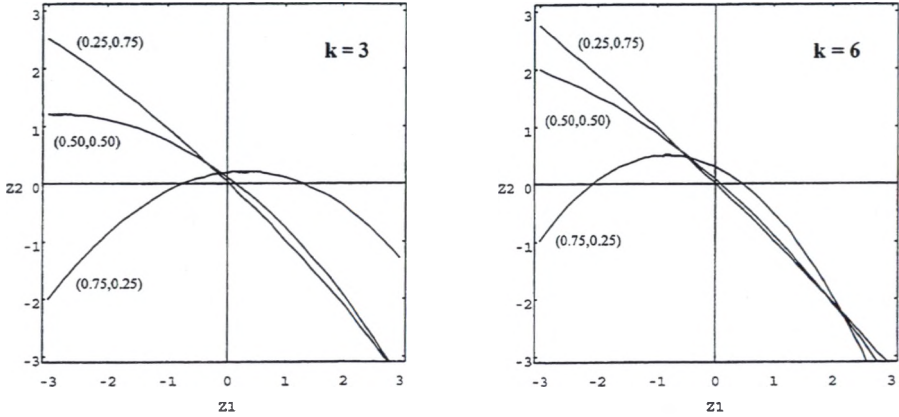
### Effect of the shape of the acquisition function

Figure 2: Acquisition function F for different values of k.



The form of the acquisition function F in (3) depends on parameter k. For larger k, the function will approach 1 more quickly as  $L_1^*$  and  $L_2^*$  increase. Figure 2 shows the acquisition function with values of 3 and 6 for k. Regression lines for the regression of  $z_2$  on  $z_1$  are given in Figure 3 for different values of s and t in (1). Comparison of the sets of curves in the left and right parts of Figure 3 show that the two different forms of the acquisition function investigated here do not produce vastly different relationships between  $z_1$  and  $z_2$ . With the more extreme curve ( $k=6$ ), the relationship is in general more negative but otherwise the shape of the curves is more determined by the values of s and t.

Figure 3: Regression curves for regression of  $z_2$  on  $z_1$  (both traits standardized) with different forms of the acquisition curve (determined by parameter  $k$ ). Values in brackets denote  $(1-s, 1-t)$  and give the proportions of the acquisition process and allocation process controlled by the mechanisms described in (3).



For interpretation of the curves in Figure 3 we have to remember that function  $F$  (responsible for the acquisition process) introduces a positive and function  $G$  (responsible for the allocation process) produces a negative relationship between the two traits. If the proportion of resources acquired through  $F$  (first of the two numbers between brackets in Figure 3) is small and the proportion of resources allocated to either of the two traits through  $G$  (second number) is high, the relationship is negative and the deviation from linearity is small. In the opposite case (big effect of  $F$ , small effect of  $G$ ) the relationship is clearly curvilinear. In this case, at low levels of  $L_1^+$  and  $L_2^+$  an additional +allele at  $L_1$  will have an enhancing effect not only on  $z_1$  but also on  $z_2$  as the additional availability of resources will outweigh the shift of resources away from  $z_2$ . At high levels of  $L_1^+$  and  $L_2^+$ , the allocation process becomes dominant yielding a negative relationship between  $z_1$  and  $z_2$ .

*Acquisition of resources influenced by only one set of genes*

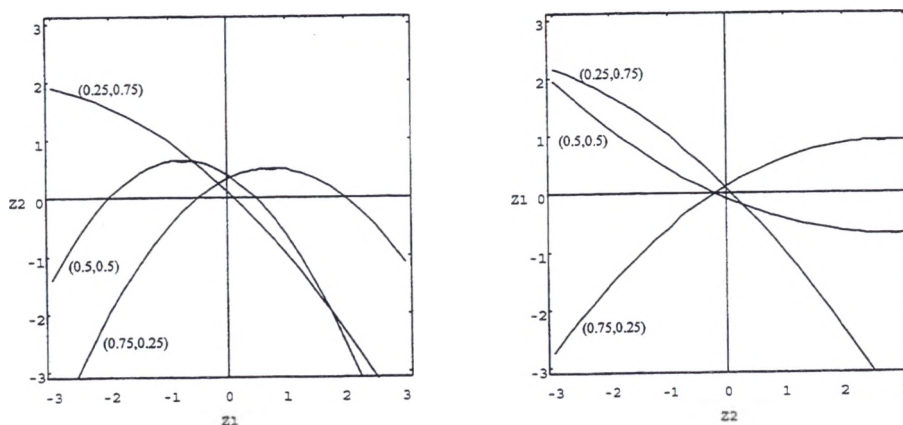
With definition of  $F$  and  $G$  as in (2) we assume implicitly that the  $L_1$  and  $L_2$  gene complexes are of equal importance, for the acquisition of resources as well as for the allocation of resources. Various deviations from this assumption are imaginable. Here we shall consider the case where  $F$  in (3) is replaced by

$$F = 1 - \exp(-kL_1^+) \tag{4}$$

so that only the  $L_1$  loci are involved in the acquisition but loci from both sets determine the allocation of resources. Unlike in the earlier example it matters in this case if we regress  $z_1$  on  $z_2$  or vice versa. Figure 4 gives both types of regression curves for  $k=3$  and varying  $s$  and  $t$ . When we take  $z_1$  as the independent variate, the curves are somewhat similar to the previous ones (Figure 3), but more curved. This is what we expect as for low  $L_1^+$  trait  $z_2$  is profiting more from an increase of  $L_1^+$  (yielding an increase in resources). When  $z_2$  is the independent variate, the curves are less easy to

understand as we are interpreting against the causal flow. The regression lines are generally less curved and sometimes concave (positive quadratic term).

Figure 4: Regression curves for  $z_2$  on  $z_1$  (left) and  $z_1$  on  $z_2$  (right) when acquisition of resources is only influenced by genes from the  $L_1$  complex. For definition of values in brackets see Figure 3.



#### DISCUSSION

The results show that substantial curvilinearity in the relationship between two traits competing for resources may arise from the model under consideration. Even if the model is too simple or wrong there is reason to believe that physiological limitations and feedback mechanisms cause curvilinearity in the genetic relationships between traits. It seems therefore worthwhile looking for such relationships. The model shown here will be used in simulations to evaluate different approaches of estimating curvilinear genetic relationships.

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