Impact of selection environment on the evolution of environmental sensitivity.

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Consequences of selection for productivity in a particular environment on performance in other environments have been investigated using a resource allocation approach. Environments were defined by the percentage of energy intake required for fitness. Insufficient energy for fitness reduced fertility and increased mortality. Animals that died had zero production. Resource intake, production potential and allocation of resources were assumed to be heritable and genetically uncorrelated, whereas fitness and (observed) production are resulting parameters. A base population was placed in a poor, intermediate, or good environment and selected for 50 generations using stochastic simulation. Resource intake was either unlimited or limited to 150% of the initial population mean. Every fifth generation, production was recorded in all environments and reaction norms were derived accordingly. Results show that selection in a good environment causes increased environmental sensitivity, as illustrated by an increased slope of the population average reaction norm, occurring especially when resource intake was limited. These results are supported by analysis of real data available in literature.

Introduction

Studies in both evolutionary biology (e.g. Stearns and Hoekstra, 2002) and animal breeding (e.g. Kolmodin, 2003; Rauw et al., 1998) have shown that longer term selection for production in a single environment will increase the *environmental sensitivity*: the animals become more susceptible to a change in the environment. In general, resources (feed intake, oxygen, etc) need to be divided over a number of processes that change throughout the animal's life. These processes include maintenance, growth, and reproduction, where maintenance includes being able to respond to changes in the environment such as an infection, shortage of food, flight reaction, etc. (Stearns and Hoekstra, 2002). In animals with increased environmental sensitivity, resources available for responding to a change in the environment are not sufficiently available. The fraction of resources that should be allocated to fitness depend on the environment. In a poor environment, more resources are required for maintaining body temperature, fighting off infections, compensating for lack of rest, etc.

At times resources are limited and trade-offs are required. These trade-offs can be divided into the ones that occur in all animals' lives (e.g. resources allocated to growth or health in growing animals), or are reproduction induced (i.e. pregnancy and lactation), and the ones that are environment induced (stress situations). Stress situations can be divided into acute and continuous stress. Acute, short-term stress situations, such as fright or infection, but in a way also pregnancy and lactation, are not specific for a single environment. They require the ability of an animal to instantly re-allocate resources to cope with the stress. This often is at the expense of other processes, as it is only for a limited period of time. The animal should be able to restore these resources afterwards. Some animals have a 'buffer capacity' in the form of extra fat and/or muscle tissue, which they can draw upon in times of need (e.g. acute stress). It seems that these animals often are better able to respond to acute stress. This could indeed be due to the fact that they have a 'buffer capacity' so that energy is readily available when needed. It could also be due to the fact that these animals importantly re-allocate resources from production, rather than from fitness related traits. Most likely it will be a combination of the two.

Even in a relatively constant, high quality environment, generations of directional selection will result in increased environmental sensitivity. This is because selected animals allocate resources to fitness related traits more often around the limits created by the environment. Consequently, selection pressure is created by the environment that counteracts the directional selection, as only animals in reasonable condition will be able to grow or reproduce. Animals that run into problems as a result of insufficient resources assigned to fitness can be considered in continuous stress. Often this involves part of the population. In case of a defined limit set by the environment, for example a feed intake limit, often most of the population will be experiencing continuous stress as a consequence of selection for increased production.

In this paper we present an extended version of the model as described by Van der Waaij (2004), that provides insight in a possible mechanism through which environmental sensitivity develops. It provides a possible mechanism for re-allocation of resources in times of acute stress. It also shows consequences of (introducing) a selection limit such as limited feed intake, a problem that seems to occur for example in dairy cattle (Veerkamp, 2002). The results will be illustrated using reaction norms.

Materials and methods

Model

Point of departure was the model as described by Van der Waaij (2004), where 'Resources' (R) are allocated according to a factor c towards 'Fitness' (F) (where fitness includes health, maintenance, and reproduction), and (1-c) towards production. Production can be divided into 'Production Potential' (Pp) and 'Observed Production' (Po). Three thresholds were defined for c. There is an upper threshold U_r above which all animals are reproductive and survive, but below which reproductive probability decreases. Then there is an upper threshold U_s below which survival probability decreases. Finally there is a lower threshold below which all animals die. Both probabilities are 1 at the respective upper thresholds and linearly decrease to 0 at the lower threshold. Observed production in between thresholds is equal to the reproductive probability times Pp.

This model was extended by allowing the animal to develop a 'Buffer capacity' (buffer) in times of relatively low metabolic demands. In addition, the model now allows for the presence of, and response to, 'Acute Stress' (AS). Acute stress is defined as a factor that may vary in size and duration, and that draws upon resources already allocated to production and fitness related traits. In other words, acute stress creates a demand for re-allocation of resources, where the proportion of resources re-allocated from fitness is denoted as d (and from production as (1-d)). Also, the model allows for the presence of a limitation to resource intake (e.g. physiological limit). All traits are expressed in energy units. In this paper only the additional features will be described. For details on the model we refer to the original paper.

It is assumed that in a good environment, a smaller proportion of resources is required for expression of full fitness potential than in a poor environment (e.g., temperature difference, disease pressure). In a good environment, animals that allocate more energy towards fitness (Rf) than strictly required for maintaining health and reproduction (Rf_demand) will be able to develop some energy storage that can serve as buffer capacity in times of acute stress. In a poorer environment fitness related traits will create a larger energy demand and fewer animals will allocate sufficient amounts of energy towards fitness to build up some buffer capacity.

buffer = Rf – Rf_demand

In some situations, acute stress will occur. This is defined as a situation where an amount of energy is required to cope with the sudden change in the environment relatively quickly (e.g. cold/heat stress, infection). Increase in feed intake to meet this demand is not possible as maximum feed intake is already assumed to be expressed. Animals that have a buffer capacity will use this energy first to meet the acute stress demand. The remaining energy requirements need to be re-allocated from fitness and production. Each animal is assumed to have a heritable re-allocation factor d, determining what fraction of the energy demanded by the acute stress has to come from fitness (d) and what from production (1-d). It was assumed that all resources indeed are re-allocated, if not, the animal would die from the consequences of the acute stress. Consequences of re-allocation are determined by the environment as the resources allocated to fitness need to remain sufficient to survive, also after the re-allocation of resources towards the acute stress. In this model the duration (time) is not of influence on the survival and reproduction, so that it could also represent multiple times of acute stress at time intervals. The size of the stress, however, is of influence of the chance of reproduction and survival, as the energy needs to be re-allocated, irrespective of the duration of the stress. The animals are selected on the observed production averaged across the periods with and without acute stress. It was assumed that feed intake was not influenced by the acute stress or the environment. It was assumed that c, d, Pp, and R were uncorrelated.

Population and Parameters

An initial population was simulated with 240 males and 240 females. In total 65 discrete generations were simulated (200 replicates). During the last five generations random mating was applied so that the counteractive force of selection by the environment (here called natural selection) would become visible. During the first 60 generations, in each generation the aim was to select 15 males and 60 females on their own performance for total lifetime observed production (mass selection). So selection was performed after possible acute stress. No adjustment was made to the maximum number of offspring per female, or to the maximum number of females selected, even if the desired number of selected animals could not be met, sometimes resulting in a fluctuating population size. Each dam had a maximum of eight offspring. Each offspring born had a probability of 0.5 to be male, otherwise it was female.

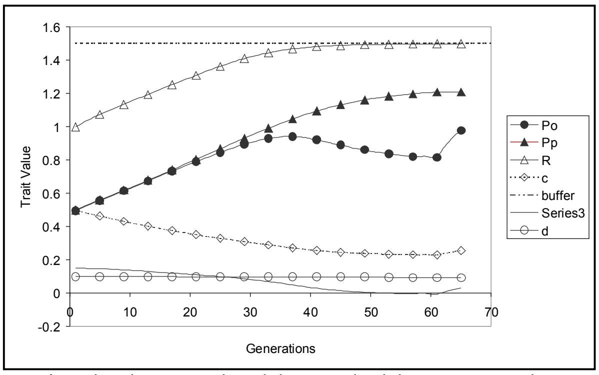
Mean and phenotypic SD were 0.5 and 0.05 for Pp, 1.0 and 0.1 for R, 0.5 and 0.05 for *c*, and 0.1 and 0.05 for *d*, respectively. The heritabilities for Pp, R, c and d were set to 0.3. Three types of environments were assumed: a good, a medium, and a poor environment, indicated by the values of the thresholds. The values for the thresholds were chosen such that in the poor environment 67% of the animals showed full reproductive performance. Acute stress was varied 0% or 30% of the resources required for 0% or 3% of the time. Animals were either fed ad lib at all times, or until a limit was reached of 150% of the average initial resource intake value (i.e. 1.5).

Results and discussion

Continuous stress

In Figure 1 are the population means across generations for the various components, in a situation where there is a limit to resource intake, but no acute stress and the population is kept in a good environment. Selection for observed production creates selection pressure on resource intake and allocation of resources towards production. During the first 20 generations little or no metabolic stress occurs and the resource allocation factor can be reduced without punishment, consequently also reducing the buffer capacity. This is no problem as there is no acute stress. Problems develop around generation 25, when the allocation of resources away from fitness, in favour of production, has pushed the population towards the limits set by the environment. This is illustrated by the deviation of observed production from production potential, as there will be a reduction in observed production by animals with c below the thresholds and some animals may have died. Subsequently, the population reaches the maximum resource intake level and strong metabolic stress develops. This is illustrated by the decrease, rather than increase in observed production from approximately generation 35 onwards. When selection for observed production is relaxed from generation 60 onwards, indeed no increase in production potential is observed. However, a strong increase in observed production, and to a lesser extend in the resources allocated to fitness, illustrate the natural selection force favours

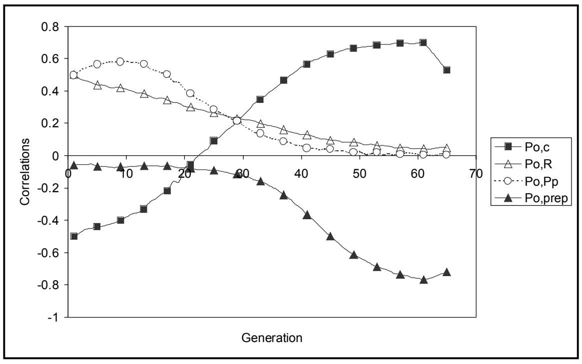
Figure 1. Population means of the model components and observed production.



animals that are healthy and able to reproduce (and thus survive).

In Figure 2 are the correlations between observed production and production potential, resource intake capacity, resource allocation factor, and reproduction probability. Because some of the animals had a reduced reproduction probability from the beginning, the correlation with observed production is slightly negative. However, from approximately generation 25 onwards the correlation decreases, representing the development of environmental sensitivity. The correlation between observed production and resource allocation factor increases rapidly until approximately generation 50, after which is slows down. Simultaneously, the reproductive capacity of the population has reached the stage that replacements cannot be met due to insufficient reproductive performance (results not shown). The correlation between observed and potential production clearly indicates at which point in time the population reaches the limit set by the environment. Observed production then becomes increasingly dependent also on allocation of resources. In other words: the genetic background of observed production changes across generations. After removal of the selection pressure on observed production, natural selection causes a shift in resource allocation from production to reproduction as indicated by the change in correlations.

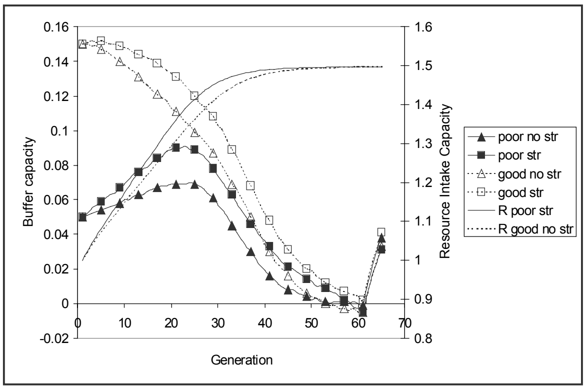
Figure 2. Correlations between observed and potential production, resource intake capacity, resource allocation factor, and reproduction probability production across generations



Acute stress

In Figure 3 is the change in buffer capacity across generations, both in good and poor environment and with and without acute stress, when selection is on observed production. As the initial population was the same in all situations, in the good environment more resources are available to create a buffer than in the poor environment. Within environment, the upper line represents the situation with acute stress. In the poor environment, initially the buffer capacity increases, both with and without acute stress. The latter is a consequence of indirect selection for increased resources assigned to fitness, resulting in increased buffer capacity for some animals. In the poor environment, animals that assign large proportions of their resources to fitness are more likely to survive and reproduce. Therefore, strong selection pressure is on c initially. In the good environment initially there is no selection for increased resources for fitness and the buffer is emptying, also though more slowly, when acute stress occurs. As strong metabolic stress develops, selection pressure on reduction of resources for fitness increases and the buffer is emptied in both environments. In situations with acute stress, this occurs a few generations later than in situations without acute stress. Release of selection on observed production results in a rapid increase in buffer capacity (see figure) and reproductive capacity (from <4 in generation 60 to 6 in generation 65).

Figure 3. Change in buffer capacity across generations, both in good and poor environment and with and without acute stress

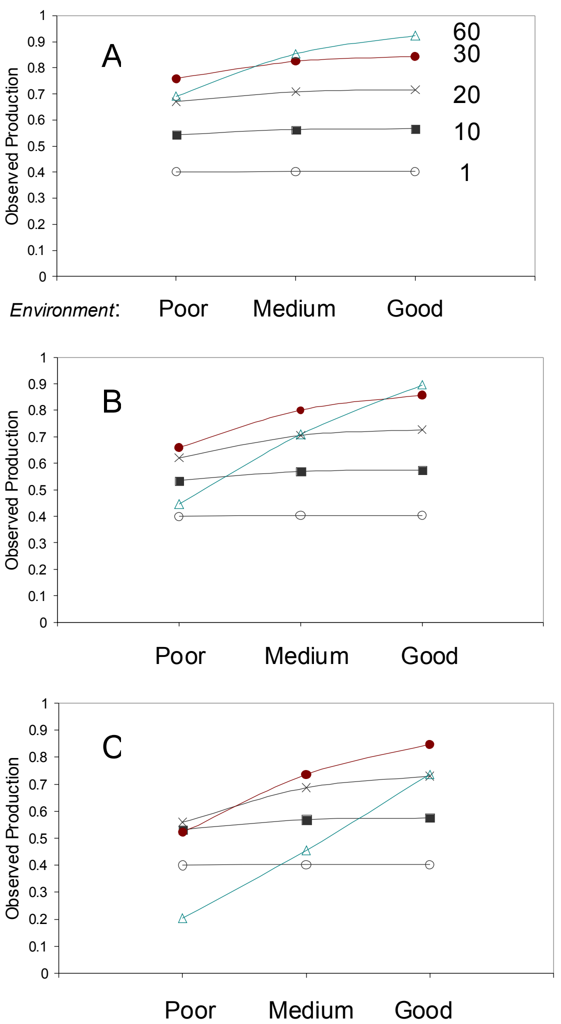


Reaction norms

In Figure 4 are the consequences of transfer to a different environment when selection was in a poor, medium, or good environment. Figure 4A shows consequences of selection in a poor environment. During the first approximately 20 generations sufficient resources are allocated to fitness and the poor environment is not limiting yet. In generation

30 the population is pushed towards the thresholds and improvement of observed production is reduced. By transferring the animals to an improved environment, the performance is increased to the potential level again. Then the resource intake limit is met and selection for observed production causes a decrease in the amount of resources available for fitness in favour of production. Consequences are reduced reproduction and survival rate and thus a decrease, rather than an increase, in average observed production. Transfer to an improved environment again improves the situation. In Figure 4B the animals are selected in an environment of medium quality. After generation 10, transfer of those animals to the environment of poor quality results in reduced performance. In generation 60 the performance in the poor environment of animals selected in the medium environment is not much better than in the initial situation, and even worse than in the initial situation for animals selected in the good environment (Figure 4C). Figure 4 clearly shows that G×E interaction develops as soon as insufficient resources are assigned to fitness to have full survival and reproductive performance.

Figure 4. Reaction norms for animals selected in a poor (A), medium (B), or good environment (C), evaluated at 1, 10, 20, 30 and 60 generations of selection on observed production.



Conclusions

- The selection environment should be of equal or less quality than the environment the selection is aimed at.
- Environmental sensitivity develops under metabolic stress and can be elevated by improving the environment
- The selection environment importantly determines the direction of selection on the underlying traits.
- Selection pressure on buffer capacity is highest in a poor environment and in the presence of acute stress
- Selection pressure on observed production in the presence of acute stress results in reduced re-allocation of resources away from fitness, especially in the presence of strong metabolic stress.

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