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Selection for 'environmental fit' from existing domesticated species

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Summary
The selection of farm animals through breeding for human benefit has a very long history. In more recent times the practice of animal breeding has become highly sophisticated and the speed of change in 'production traits' such as rate of growth and milk yield has correspondingly increased dramatically. This narrow focus on production traits led to a number of well-documented examples of 'unfavourable' correlated responses such as negative fertility and health issues in high-yielding dairy cattle, with concerns that animal breeding is inherently antagonistic to animal welfare. In this paper the authors explore some of the questions surrounding breeding and welfare and, specifically, how to conceptualise and improve the 'fit' between the selected animal and the environment, or system, in which the animal is reared and managed. The authors conclude that there is a need for a better understanding of genotype × environment effects on health and welfare traits in order to inform the development of breeding programmes that lead to improved environmental fit in animals. They also see the need for the development of valid traits for assessing health and welfare, greater consideration of early life effects that can also potentially affect environmental fit and a need to consider the impacts of climate change on breeding programmes.

Keywords
Animal breeding – Animal health – Animal welfare – Climate change – Early life effect – Genotype × environment interaction – Narrow breeding goal.

Introduction

'Selection' in the title of this paper refers to the field of genetic improvement of livestock by means of 'artificial selection' where humans make choices over which animals within a population should mate in order to achieve a change in the genetics of the population that is favourable for humans. Integral to such selection is a requirement to control mating, so selection is mostly applied to domesticated animals, i.e. those species whose evolutionary process has been influenced by humans to benefit humans. There are many examples of this, which range from selecting farm livestock for production traits to changing behavioural traits in companion animals (1).

Selecting for 'environmental fit' implies that we are aiming for a good match between the end result of the selection process, in terms of genetic change, and the environment, or system, in which animals are reared and maintained. In the context of this paper the authors are especially focusing on health and welfare outcomes. Under conditions of natural selection a close correspondence between animal genetics and the environment is at the core of evolutionary 'fitness' (see Fig. 1a), i.e. the capacity of animals to survive and reproduce and hence pass on genes to the next generation. In the absence of any other supporting mechanisms, wild animals that fail to adapt successfully to environmental change will become extinct, albeit usually over extended periods of time.

The situation for domestic animals is somewhat different. Three points highlight this. First, the environments in which they are kept can change rapidly, subject to human-orientated 'drivers' (Fig. 1a [i]). This is illustrated by the intensification of farm animal housing systems that occurred after the Second World War, inspired by the aim of producing more and cheaper food. As pointed out previously (2), it can be argued that such intensive environments are often not well matched to the animals' evolutionary adaptations. An example is the use of crates to house parturient/farrowing sows. Farrowing crates are known to interfere with the behavioural adaptation of sows

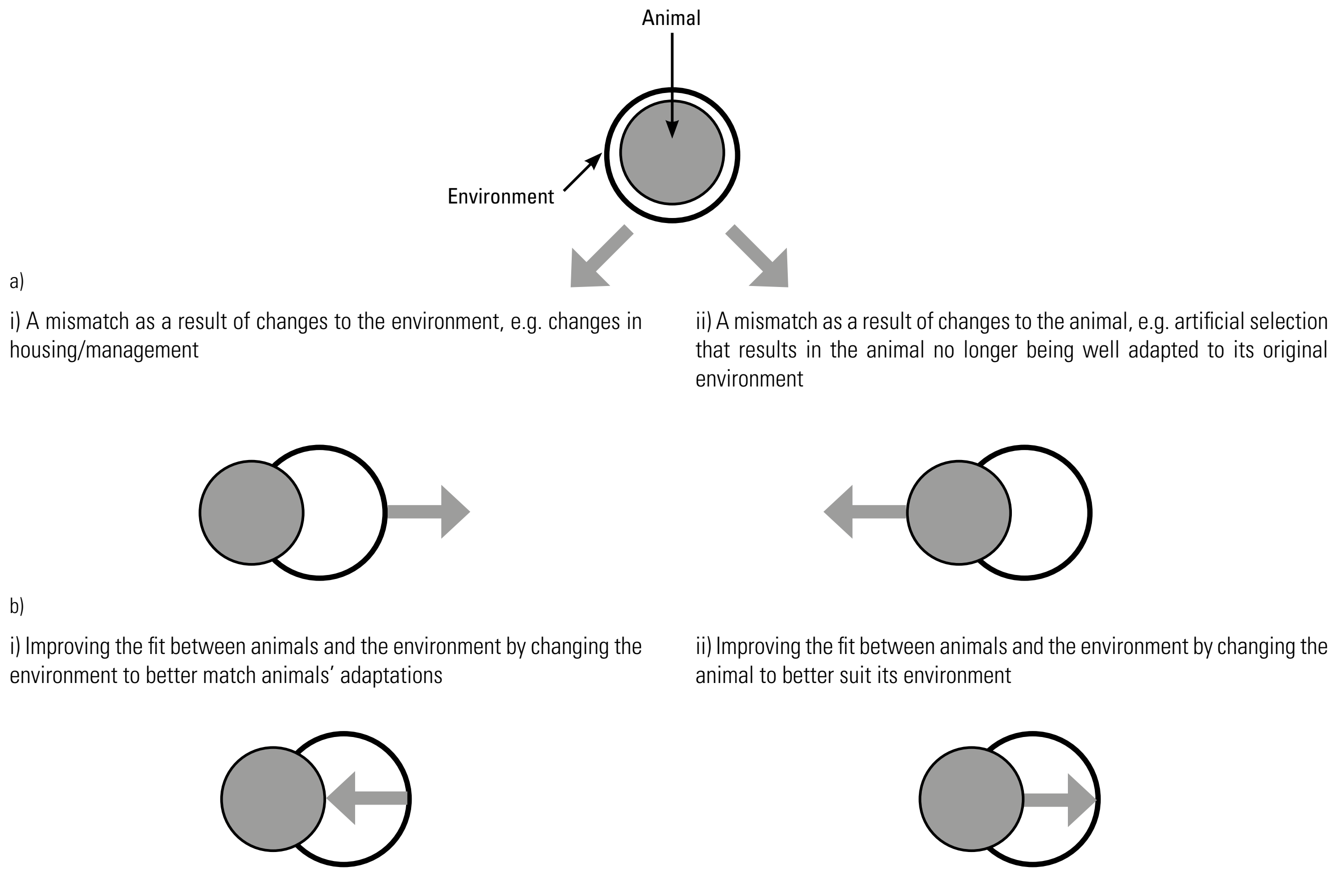


Fig. 1
Mismatches between the animal and its production environment and the general 'solutions' for reducing such mismatches

to build a protective nest for their litters; sows housed in crates are still activated to nest-build but are physically prevented from doing so and as a result show behavioural and physiological indications of 'stress' (e.g. see Jarvis *et al*. [3]). Second, as animals are being selected continuously (e.g. for increased production), it is also possible to argue that the process of artificial selection itself will change the environmental requirements of selected animals (Fig. 1a [ii]). Third, because domestic animals have a 'support system' involving interventions by human owners/carers, it is possible for adverse impacts of any mismatches between the animal and environment to be ameliorated or buffered and thereby 'tolerated' within the production system. An example of this is the effect of detrimental adaptations on lamb survival in lowland sheep breeds, which is mitigated by a higher level of human intervention at lambing than is required for hill breeds (4).

There are two well-discussed strategies that can be used to rectify such mismatches between domestic animals and the environment in which they are housed and managed (Fig. 1b [i] and [ii]). First, we can change the environment to better suit the animal (5) or, second, we can select animals to be better suited genetically to the environment we have chosen for them. The first of these options has long been the one favoured by those concerned with animal welfare. For example, the thinking behind systems such as the Edinburgh Family Pen for pig production was to accommodate as much of the animals' 'natural' behaviour as possible within a housing system (6). The second option, i.e. selection for behaviour traits, has been criticised as being potentially unethical (see [7] for a review of these issues).

In this paper, the authors will look at this second option of selecting animals for better environmental fit, but here the scientific and practical issues that underlie this approach will be emphasised.

Genes or environment or both?

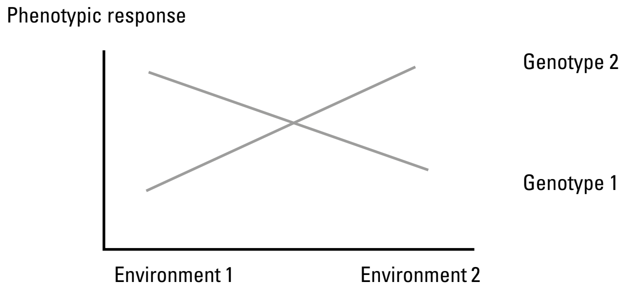
The question of improving the 'environmental fit' through selective breeding raises important issues for animal breeding and also for the overlap between animal welfare and breeding.

The primary focus of selective animal breeding has been on increasing the productivity of domesticated animals, leading to substantial increases in yield from most species (1). Unforeseen consequences of such narrow production-focused selection became apparent in the 1980s and 1990s when correlated effects on other traits were identified. A number of examples of these 'undesirable effects' have been discussed, including the wider effects of selection for milk production on health and welfare traits in dairy cows (8). The effect of narrow breeding goals will, in principle, affect animals equally in all production environments and can be seen as contributing to reducing environmental fit.

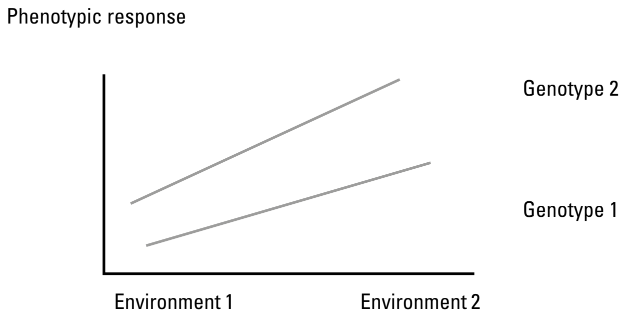
A second issue associated with selection of animals to better fit an environment is the extent to which genes and the environment interact to influence traits of interest, including those affecting health and welfare. Genotype × environment (G×E) interactions have been much studied in population genetics and in plant and animal breeding (for a review, see [9]). The response of a genotype to a change of environment has been characterised using 'reaction norms', and two types have been identified (10) (Fig. 2). In principle, both types of reaction norm can have implications for animal breeding decisions. The first, a scaling G×E effect, is where genotypes respond to conditions in different environments but there is no re-ranking of the genotypes. Such effects indicate that genotypes vary in their 'sensitivity' to environments, thereby providing options for choosing sensitive or insensitive genotypes to suit specific environmental conditions. The second, a re-ranking of genotypes, occurs where the genetic control of a trait differs across environments. In such cases it may be appropriate to select for genotypes to suit specific environments.

Whilst G×E effects have been much discussed in animal genetics and breeding, there has been a continuing debate over their importance in practice; some results indicate that G×E effects are relatively unimportant (11), whilst others firmly support the existence and relevance of G×E interactions (12, 13). One reason for these conflicting results is the scale of the differences between the genotypes and environments being studied. In studies where the same genotype of animal is used across a range of environments (such as occurs with the global distribution of dairy bull semen) there tends to be evidence of strong G×E effects (e.g. 14). In addition, interest in G×E effects has previously been focused on production traits (e.g. feed conversion efficiency and milk yield), which tend to have moderate to high heritability, as opposed to welfare-relevant traits (e.g. health and fertility), which often have lower heritability. As a rule, traits with low heritability will be more sensitive to G×E interaction than more highly heritable traits (15). Hence G×E interactions have not previously been a major focus of animal breeding practice. Moreover, it has been reasonably common practice for selection to take place in one environment and rearing of offspring in another. For example, selection of laying hens may take place in single cages so that egg production can be measured, whereas production birds may be housed in social groups, a practice that is seen to be at least partly responsible for the development of production problems such as feather pecking (16).

More recently there has been growing interest in selecting for traits in farm animals that are variously described in terms of 'adaptability', 'plasticity' or 'robustness' (17). Interest in robustness stems partly from the concerns we have already noted that relate narrow selection goals to health and welfare outcomes in farmed animals. However, robustness also links to G×E effects, as it has been interpreted as applying to adaptability across environmental conditions (e.g. 18, 19). There are also strong links between this interpretation of robustness and concepts of animal welfare, where the 'adaptation' of the animal to its environment has always been a major focus. Methodologies for exploring the concept of robustness have been published (20) and applied to different livestock scenarios (21, 22, 23, 24). Figure 1 illustrates one of the main welfare concerns, i.e. that intensive farming environments are not matched to the animals' evolutionary



a) A genotype × environment interaction causing 're-ranking' of genotypes across environments. In such a scenario there is no obviously superior breed and specific breeds should be bred for the two environments



b) A genotype × environment interaction resulting in a change of scale in the phenotypic response of the genotypes across environments. In such a scenario Genotype 2 is said to show greater environmental sensitivity than Genotype 1 and the degree of environmental sensitivity of genotypes could be taken into account in breeding for increased environmental fit

Fig. 2
Reaction norms of two hypothetical genotypes to different environments (systems of production)

adaptations. In a similar vein to the debate on breeding for robustness, animal welfare researchers have suggested that some welfare concerns could be addressed by breeding for 'general adaptability' traits such as reduced 'fear' or 'stress' responses (25), whilst others (26) have pointed to ethical issues with this approach, such as the potential risks of selecting for reduced sentience in farm animals.

This section has illustrated that animal breeding has in recent years come closer conceptually to recognising the importance of the match between animals and the production environment and in that sense is also more closely aligned to animal welfare concerns. In the next section, the authors will discuss briefly some of the opportunities that could be used to increase environmental fit through animal breeding practice.

Solutions

Broadening breeding goals

The solution to the adverse effects of narrow breeding goals is to 'broaden' them in order to reduce the focus on increasing productivity and to include other traits such as those relating to the animals' health and welfare (27). Clear examples of the benefits of this approach come from dairy cow breeding, where it is possible to track how the relative weights assigned to production and to health and welfare traits have changed over time to favour health and welfare traits (28). However, industry/sectoral uptake of such a broadening of breeding goals can be limited by pressure to justify changes to breeding goals primarily in economic terms, whereas the justification in fact involves a mix of economic and non-economic considerations (29). As the greater emphasis on breeding goals associated with non-production traits continues, methodologies for estimating social and wider values are being developed (30).

Utilising genotype × environment effects

In terms of solutions to bring G×E effects more into focus in animal breeding the authors would suggest the following.

Measurement of health and welfare traits

Our increasing awareness of the impacts of animal breeding on welfare stems in part from the introduction of novel and relevant traits. This is especially apparent for dairy cow breeding, where the introduction of fertility and health traits has helped to identify the need for action to reverse negative genetic trends in these traits (31). At the moment, we are often constrained to use what we can measure on farm on a large (national or international) scale, as opposed to what we should measure. To fully understand and explore G×E interactions and/or animal 'robustness', it is also important to define the environmental range and scale of the production systems and how they may change (management factors, weather events) over time (32). Many studies have been limited in their ability to define key 'environmental phenotypes' in commercial data sets and until this limitation is overcome we may not be able to accurately identify the key environmental factor(s) that limit animal performance (33). In animal welfare terms there is also arguably a need to develop 'animal phenotypes', or traits, that more directly assess the animals' experiences (e.g. 34).

Improving understanding of genotype × environment effects

As a more thorough understanding of the impacts and relevance of G×E effects would better inform animal breeding strategies, there is a clear need for more research to estimate reaction norms for important health and welfare traits. For example, a recent study found that, whilst most daughters of dairy bulls showed an increased lifespan in less intensive units, a small number of bulls had daughters that were relatively insensitive, in terms of their lifespan, across systems (35). This would indicate the possibility of farmers being able to select appropriate sires for specific environments. In other work, breeding values for piglet survival measured in an indoor system using farrowing crates were generally predictive of piglet survival in an outdoor system, suggesting a lack of G×E effects and the possibility that a single breeding programme could provide animals for these divergent environments (36).

Controlling rearing conditions for parents

In light of increasing evidence that pre-natal conditions can alter development in offspring and also potentially have trans-generational effects (37), it is becoming more relevant for the rearing conditions of parents to be controlled and measured in order to take early life effects into account in breeding evaluations. The development of biomarkers that provide an integrated assessment of early life challenges could be especially useful in this sense (34).

Indirect genetic effects

The changes that have been realised through artificial selection have resulted mainly from additive or direct genetic components of individuals that have been translated from generation to generation on the basis of selection decisions. However, there are also some non-additive or indirect genetic effects that can affect performance at the population level. An indirect genetic effect now being explored in livestock species is the concept of social breeding value (38). For example, calculations enable each member of a group of animals to be given a direct breeding value, which accounts for the individual's genetic value for a trait inherited from its parents, and a social breeding value, which accounts for the impact of the group on an individual's value for a trait; these two components can be combined to give a total breeding value (39). 'Negative' social interactions, e.g. aggression and fighting, have been shown to reduce production and the welfare of animals. Examples of the negative effects of such interactions include increased mortality in domestic chickens due to cannibalism (40) and reductions in the growth rate of fish that experience aggression (41, 42). Now that social breeding values are being calculated it is possible to estimate their impact on social behaviour and growth. Thus, for example, it has been suggested that including social breeding values when selecting for growth in pigs would, under equivalent conditions, promote the rapid establishment of dominance when pigs are first mixed, leading to a subsequent reduction in fighting immediately after the mixing period (39).

Genotype × environment in a changing world

As discussed, G×E interactions can have a detrimental impact on welfare when the production system does not 'match' the animals' genotype. In the era of international breeding companies, the range of production systems to which different genotypes of animals are exposed varies from farm to farm, region to region and country to country, and companies 'test' animals in some of the key types of production system (43). The physical environment remains fixed, to a certain extent, but there are changes over time that genotypes need to be able to accommodate. These changes can include short-term/transient impacts on the management of animals and exposure to fluctuating environmental conditions (44), including extreme weather events as well as long-term climate change (45). It is this latter longer-term temporal form of G×E interaction that breeding goals, and the groups/companies responsible for them, are beginning to address, in addition to the spatial differences that exist among production systems (e.g. regional differences in the types of production system, management differences, environmental/climatic differences). Breeding for unknown future production system environments requires the incorporation of layers of complexity and uncertainty in our breeding goals. However, if we are to increase the sustainability and robustness of animals and their production systems in the face of the harmful effects of climate change, we need to begin to address this. There has also been an increased interest in maintaining the present diversity of animal genetic resources (AnGR) so that we can utilise them for some unknown future, be it as a result of climate change or some other major global driver (46).

Conclusions

Animal breeding has been blamed for a number of the welfare issues that have emerged since the Second World War. Whilst there are important lessons to be learned from the past there is also considerable opportunity now to use animal breeding to improve animal welfare. This will depend in part on discarding the assumption that selecting animals to suit environments, as opposed to selecting environments to suit animals, is necessarily wrong. This review highlights the need for a better understanding of the role of G×E interactions in affecting the expression of health and welfare traits in order to provide a sound basis for the development of breeding programmes. Strong evidence of G×E interactions would suggest the need for genotypes to be bred within specific systems. Alternatively, evidence that genotypes vary in their sensitivity to environments would provide another option for farmers to better match genotypes to particular systems without the need for within-system breeding. Other needs highlighted here include the development of validated traits to assess health and welfare, and also the requirement for greater consideration of early life factors in breeding programmes where they can be shown to be relevant.

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Sélection des traits d'« adaptation environnementale » chez les espèces animales domestiques

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Résumé

La reproduction sélective des animaux d'élevage est une pratique très ancienne destinée à améliorer la rentabilité des élevages. Plus récemment, l'amélioration génétique est devenue extrêmement sophistiquée et la rapidité avec laquelle certains « traits de production » sont modifiés, par exemple la vitesse de croissance ou la production de lait, a augmenté de manière exponentielle. La sélection axée sur les seuls traits de production a entraîné l'apparition de réponses indésirables liées à cette sélection, qui ont été bien étudiées : il peut s'agir par exemple de problèmes de fertilité ou de santé affectant les vaches laitières de fort rendement. Il est à craindre, au vu de ces corrélations, que la sélection animale et le bien-être animal ne présentent des caractères intrinsèquement antagonistes. Les auteurs explorent certaines questions liées à la sélection animale et au bien-être animal, notamment comment définir et améliorer l'adéquation entre, d'une part, un animal issu d'une sélection, et d'autre part, l'environnement ou le système au sein duquel il sera élevé. Les auteurs concluent à la nécessité de mieux comprendre les effets des interactions entre génotype et environnement sur les traits liés à la santé et au bien-être, afin de développer des programmes de sélection animale en connaissance de cause et d'améliorer ainsi les traits d'adaptation environnementale chez les animaux. Ils plaident également pour le développement de mesures génétiques valables permettant d'évaluer la santé et le bien-être, pour une meilleure prise en compte des effets potentiels des premières phases de la vie sur les capacités d'adaptation environnementale et enfin pour la prise en compte de l'impact du changement climatique sur les programmes de sélection.

Mots-clés

Bien-être animal – Changement climatique – Effet des phases précoces de la vie – Interaction entre génotype et environnement – Objectif de reproduction restrictif – Santé animale – Sélection animale.

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Selección de «aptitud ambiental» a partir de especies domésticas existentes

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Resumen

La selección reproductiva de animales de granja practicada en beneficio propio por el hombre goza de una larga historia. En los últimos tiempos las técnicas de reproducción animal han cobrado un carácter sumamente sofisticado, y «rasgos de producción» como la tasa de crecimiento o la producción láctea han evolucionado también, en consecuencia, a gran velocidad. El hecho de privilegiar los rasgos de producción ha dado lugar a una serie de ejemplos, bien documentados, en los que aparecen respuestas «desfavorables» correlacionadas, como problemas de fertilidad o de salud en vacas de alto rendimiento lechero, lo que plantea el interrogante de un posible antagonismo intrínseco entre selección animal y bienestar animal. Los autores examinan algunas de las cuestiones que rodean la reproducción y el bienestar de los animales, y más concretamente la manera de teorizar y mejorar la adecuación entre el animal seleccionado y el medio (o sistema) en el que se cría y crece, o dicho de otro modo, la «aptitud ambiental» del animal. Los autores llegan a la conclusión de que es necesario entender mejor los efectos que la interacción entre genotipo y medio tiene sobre ciertos rasgos de salud y bienestar con objeto de fundamentar la elaboración de programas reproductivos que puedan conferir mayor aptitud ambiental a los animales. Además, a su entender, también es indispensable determinar cuáles son los rasgos útiles para evaluar el estado de salud y bienestar, así como tener más en cuenta los efectos en las primeras etapas de la vida que puedan incidir en la aptitud ambiental y tomar en consideración la influencia del cambio climático en los programas de reproducción.

Palabras clave
Bienestar animal – Cambio climático – Efecto en las primeras etapas de vida – Interacción entre genotipo y medio – Objetivo de reproducción excesivamente restringido – Reproducción animal – Sanidad animal.

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