

# Are there limits to selection in poultry? Alternative production and local breeds.

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Selection response still takes place in poultry after 50 generations of selection or more. The mechanisms maintaining selection response in closed populations may involve recombination, mutation and epistatic interactions. Furthermore, the continuous addition of new selection criteria can delay the possible limit associated to single trait selection. Selection response is mainly threatened by inbreeding which occurs as a consequence of a narrow genetic base and/or a poor management of genetic variability within the population. Biological limits are encountered because of unfavorable correlated responses on fitness traits to a point that the survival of individuals can be affected. Biological limits induced by extreme performance can be overcome by adapting the breeding program, introducing new selection criteria, changing the management or developing remedial technologies. Extreme situations affecting bird welfare raise ethical issues. Ascites in broilers or spontaneous bone breakage in layers are painful and one may question whether such pain is justified by the human need for protein consumption. Regulations or market requirements may be set up to limit the performance at a level which is compatible with animal welfare, resulting in a voluntary limit to selection. Furthermore, highly performing animals need high quality diets, which diverts food resources from humans and may not be sustainable. Alternative systems, using local breeds or strains with less extreme performance, or dual-purpose birds, are better considered by consumers but have a higher cost. There is no perfect system and a diversity of systems is probably the way towards sustainability. In any case, breeding objectives have to integrate environmental impact, genetic diversity, capacity to use suboptimal feed sources, in addition to production level, product quality, health and welfare status. Overall, poultry production systems can be viewed as special ecosystems, delivering services but also impacts to human societies, that need to be balanced to improve robustness of the food system.

**Keywords:** selection; fitness; welfare; ethics; environment; sustainability; diversification;

## Introduction

Domestication of chickens started several thousand years ago, and led to the diversification of domestic breeds which have populated the whole earth by migrating together with human populations. On an evolutionary scale, domestication and, even more, strong selection for increased production levels represent a very short period of time. Even shorter is the period where molecular genetics has been developed, since the 1990s, with a major impact on animal breeding, including the characterization of genetic diversity. At that point, one may question whether this can go on forever, in which conditions, for which food system? This paper first analyzes the various mechanisms or factors that can limit selection response, and examined the possible strategies to handle such limits, including the use of local breeds.

## 1. SELECTION THEORY AND POSSIBLE LIMITS

### 1.1. PRINCIPLES

Selection theory has been established only a century ago and has been applied at a large scale in poultry breeding. The power of this theory is that it relies on a simple and generalist model, the infinitesimal model, which sets the hypothesis that a large number of genes, each of them having a small additive effect, is controlling the variation of a quantitative trait. Allelic effects are considered to be independent from one gene to another and assumed to be normally distributed, so that the genetic value of an individual for a trait is simply the sum of allelic effects at all genes. The genetic value cannot be measured directly and is estimated by comparing the performance of related animals, the higher the similarity between related animals, the higher the contribution of additive genes. Successful selection is thus expected to progressively increase the frequency of favorable alleles, so that selection should reach a plateau when all favorable alleles have been fixed. At that stage, variation of performance just reflects environmental variation and there will be no more response to selection: the limit will be reached. The smaller the initial population size, the faster the limit will be reached. The history of the concepts underlying animal breeding has been revisited by Hill and Kirkpatrick, (2010), from the viewpoint of evolutionary biology. Referring to Robertson, (1960), they reminded that “*half of the ultimate (selection) response occurs by 1.4Ne generations*” where  $N_e$  is the effective population size. Thus, for a population with a  $N_e$  of 40, which is rather small, selection response should still take place after 56 generations. Since poultry lines generally have a  $N_e$  value higher than 40, no selection limit is expected at present.

Yet, real selection differs from theory for several reasons:

- Selection plateau can be expected if the selection objective stays always the same, but as soon as a new trait is added in the selection objective, different genotypes may perform better and the set of most favorable alleles will change;
- Selection plateau is tightly associated with the additive model, which is an oversimplification of genetic reality, ignoring dominance and epistasis; as soon as interactions between genes take place, the ranking of genotypes will change, and these interactions will contribute to maintain genetic variation;
- Furthermore, if allelic effects of a given gene are influenced by alleles of the neighboring genes, the genetic value of an individual will be modified when recombination occurs and modifies the ‘neighbor alleles’;
- New alleles may arise by mutation, but this phenomenon is rare.
- Allelic effects may depend on the environment where the trait is measured, genotype x environment interactions are disturbing prediction of breeding values and may prevent fixation of a ‘best genotype’.

The lack of any selection response would correspond to a fully inbred line or to cloned individuals where all candidates to selection are homozygous for the same alleles. This is one of the reasons why inbreeding is a major concern in all breeding programs. Inbreeding induces allelic fixation at random: some inbred lines may perform better than others by chance, and most of them are likely to exhibit genetic defects. Although the occurrence of genetic abnormalities may not limit selection per se, it generally decreases the number of candidates to selection and decreases selection intensity.

## 1.2. EVIDENCE FROM EXPERIMENTAL LINES

Selection experiments are generally performed on populations with a limited size, for a variable number of generations. There are a few very long term selection experiments in poultry that would make possible to observe selection limits. The longest selection experiment for a domestic bird has been achieved by Henry Marks who selected quails on 4 wk body weight for 97 generations (Marks, 1996). Two lines were selected, one being fed on an optimal diet, the P line, the other being fed on a low protein diet, the T line. Selection response was regularly observed in the P line until generation 97, with some transient plateau, whereas longer plateau were observed in the T line, but a selection response was still observed after generation 90. Several trials were made during the experiment by deriving sublines selected with a different diet composition: it was concluded that changing the selection environment could boost selection response. The effective size,  $N_e$ , of each line can be estimated to be in the range of 70 considering the number of sires and dams used. Thus, the number of 97 generations is just getting close to  $1.4N_e$ , and no selection plateau had been observed yet.

In chickens, the longest selection experiment is most probably the divergent selection experiment on 8wk body weight, conducted by Paul Siegel and collaborators for 54 generations (Dunnington *et al.*, 2013). No selection limit was yet encountered for the high body weight line after 54 generations (with  $N_e \approx 40$ ) whereas a limit was observed in the low line, starting earlier in females than in males, with no selection response after generation 50. A similar asymmetry in selection response was observed in White Leghorn lines divergently selected for antibody response to sheep red blood cells: at generation 36, selection response was still taking place in the high line whereas a selection limit occurred after generation 12 for the low line (Zhao *et al.*, 2012).

These selection experiments showed little evidence of selection limits for high value of the trait even in a population of limited size (8 sires for each of the body weight lines of Paul Siegel). The mechanism maintaining selection response in such closed populations has not been established clearly: mutations were generally thought to have taken place, but the impact of recombination breaking critical haplotypes should also be considered. The situation was different in lines selected for low value of the trait, where selection plateau was more frequently observed, probably as a result of a physiological limit. Depending on the trait, a limit could be reached also for high values. These experiments illustrate the importance of unfavorable correlated selection responses which are creating limits to selection response for biological reasons.

## 2. LIMITS ENCOUNTERED IN HIGH-PRODUCING LINES

### 2.1. SELECTION RESPONSE, DIVERSITY AND INBREEDING

In the 20th century, the quantitative genetics theory was applied with a high efficiency to industrial chicken breeding. Very high performance level have been reached for growth as well as for egg laying in highly specialized lines which are kept in well controlled environment. The comparison of performance between commercial broilers in 2001 and a slow-growing broiler population, kept unselected since 1957, showed a 3 fold increase in body weight at the age of 84 days and illustrated particularly well the major impact of selection (Havenstein *et al.*, 2003). Commercial broilers from 2001 reached performance levels completely out of the range of the growth rate that can be observed in the wild red jungle fowl, the main ancestor of domestic chickens.

Molecular studies showed that intensive selection could result in a loss of genetic diversity at the DNA level. Whatever the type of DNA markers used (microsatellites or Single Nucleotide Polymorphisms), ranking is always the same: white egg layers, which derive from a single breed, exhibit the lowest genome variation, brown-egg layers exhibit an intermediate variation, and broilers exhibit the highest variation, whereas local breeds can be found all along the scale from low to high heterozygosity, depending on their history and population size. This trend is best illustrated by heterozygosity levels which varied from 0.2 to 0.65 with the FAO set of microsatellites (Granevitze *et al.*, 2007) and from 0.13 to 0.30 for SNPs of the 600K Affymetrix chip (Malomane *et al.*, 2019). The apparent paradox of a high molecular diversity in broilers in spite of an intense selection on growth rate may be related to the higher number of breeds used at the foundation of these lines as compared to the selection process that took place in layers.

A selection plateau does not seem to have been encountered in commercial poultry species. Inbreeding levels can be estimated by pedigree analysis and more recently by the use of molecular markers. A high inbreeding level may often lead to a low reproductive ability. This could be related to an increased frequency of deleterious alleles, such as recessive lethals. This has been recently studied in layers: a higher ratio of deleterious variants, as compared to synonymous variants, has been observed in the most inbred of three layer lines (Derks *et al.*, 2018).

### 2.2 BIOLOGICAL LIMITS TO SELECTION

There are encountered when selection is degrading fitness traits to a point that the survival of individuals is affected, selection intensity is consequently decreased and, ultimately, the population itself may be lost, suppressing any possible selection. Thus, biological limits are very much related to unfavorable correlated selection responses. Furthermore, some of the long-term selection experiments have shown the importance of a balanced use of resources to maintain the physiological functions such as growth, immunity and reproduction: when such a balance is disrupted, the fitness of selected birds will decrease.

### 2.2.1 BROILERS

Broiler selection has put a major emphasis on early growth rate since many generations. Unfavorable correlated responses have been observed on fitness traits, some of them are:

-Cardio-vascular insufficiency: selection has been applied on breast muscle, with little consideration to the supply organs, such as the cardio-vascular system needed to provide oxygen to fast growing muscle. The cardiac insufficiency syndrome with pulmonary arterial hypertension has led to ascites, a typical consequence of a biological unbalance, widely documented by Wideman *et al.*, (2013).

-Myopathies: muscle abnormalities leading to severe meat quality defects have reached a major impact since 2014 and are still not under control in 2019 as reviewed by Petracci *et al.*, (2019), all attempts reported to decrease the incidence of the so-called 'wooden breast' appear to be associated with a lower growth rate.

-Reproduction: the antagonism between early growth and reproduction may limit selection in broilers. At present, broiler breeders need to be severely feed restricted (sometimes up to 90% of their voluntary intake) in order to maintain a sufficient reproductive capacity. Feed restriction is a management solution to an unfavorable correlated response, but obviously there is a zero limit to feed restriction! As pointed out by M. Vaarst (2014), there are situations in nature where a species needs to grow very fast for a short period, with little impact on the adult body weight, which remains rather constant for the reproductive period. In chickens, this would mean selecting on the shape of the growth curve, this was shown to be possible by Fernand Ricard in France, who selected a line for a high juvenile body weight and a moderate adult body weight (Mignon-Grasteau *et al.*, 2001). This breeding approach would be worthwhile in order to avoid the biological collapse of heavy birds not being able to reproduce.

### 2.2.2 LAYERS

In layers also, unfavorable trends have affected the biological balance of the bird.

-Bone strength has become a major issue in layers, as a consequence of the major pressure put on calcium metabolism and bone remodeling for eggshell synthesis. It may be all the more an issue that the length of the laying period is now increasing. Keel bone injuries appear to be very frequent (up to 85%) in brown-egg as well as in white-egg commercial lines, with a trend for a higher prevalence in floor systems than in furnished cages (Hardin *et al.*, 2019).

-Behavioural problems with feather pecking and cannibalism are frequently encountered at the commercial stage. It had been suggested that selecting laying hens on egg number in individual cages was at the same time selecting for a higher social dominance, the most dominant bird being the one producing more eggs and thus more progeny for the next generation. Under this hypothesis, the development of aggressive behavior would represent a strong limit to individual selection for egg production. Again, management solutions have been proposed, such as debeaking or having the hens wearing preventive devices, but cannibalism and mortality still occur in free-range systems, as reviewed by Elson (2014), although these systems are expected to provide better welfare. A change in the breeding program is another approach, such as group-selection or incorporating social relationships in the prediction of the genetic value. The genetics of behavioral traits is more complex than the genetics of growth or egg production, because behavior is a matter of interactions, and this represents a methodological challenge for selection, as reviewed by Wade *et al.*, (2010).

These unfavorable effects are difficult to anticipate because the bird performance is reaching an unprecedented level where values of genetic correlations between traits are not known and probably differ from what they are with a different range of performance. A typical example of a correlation changing with the trait mean is the one between growth rate and reproduction: we have seen that poor reproduction was a limit for the low body weight line of the selection experiment of Paul Siegel, but that reproduction was also poor in heavy broiler breeders. Clearly, the correlation between growth rate and reproductive traits changes according to the level of growth rate.

## 3. ETHICAL LIMITS TO SELECTION

Ethical concerns come into perspective for various reasons. In the case of poultry, they have been raised by issues of pain and survival in highly producing birds: lameness in broilers or keel fractures in layers are painful and one may question whether such pain is justified by the human need for protein consumption. While poultry industry considers such problems as technical production parameters, citizens are quite surprised and generally shocked when they hear about it. Considering the extreme feed restriction imposed to broiler breeders, these birds are constantly feeling hungry. The absence of hunger is one of the component of animal welfare, recognized by the European Union. In other words, for the sake of economic efficiency, a chronic state of suffering is imposed to chickens during most of their life. Another major ethical issue for laying lines is the culling of male day-old chicks, which results from the high specialization of these lines and the lack of marketing value for very slow growing males. Proposing dual-purpose crosses is a way to overcome it (see also section 5): coming back to dual-purpose chickens corresponds to a selection limit for highly specialized layers.

At first, this looks to be a very emotional motivation, but it raises philosophical questions: what is the right of humans to cause suffering in other living organisms? This is quite different from the acceptance of killing animals for food. The main issue is that selecting for continuously higher performance should not induce a chronic state of pain for the animals. Is this the responsibility of breeders? The general answer is no, because they need to answer the market demand. Are the slaughterhouses, the distributors of processed food, in other words the leaders of the market demand, aware of the welfare issues occurring upstream in the production chain? Not so much. Actually, nobody feels really responsible for the painful consequences of extreme performance levels in high-producing lines, each actor of the chain tries to mitigate these consequences and there is always a good reason to say that they cannot do differently because of the market demand. That is the reason why NGOs concerned about welfare have started to act at the market level, by increasing awareness of the consumers on such issues. The most efficient action in this respect is probably the one conducted in The Netherlands at the level of supermarkets since 2013,

called the ‘Chicken of Tomorrow’: supermarkets modified their requirements to their providers with a limit imposed to the growth rate of broilers ( $\leq 50\text{g/day}$ ) together with density and environmental conditions. Consequently, the market share of slow-growing broilers significantly increased in the Netherlands up to 50% in 2016.

Ethical issues depend on the cultural background but can be a serious threat leading some consumers to reject animal products and become vegetarians, creating a very deleterious atmosphere around animal production, not only for chicken

#### 4. ENVIRONMENTAL LIMITS TO SELECTION

##### 4.1. ENVIRONMENTAL FACTORS AS A LIMIT TO PERFORMANCE: TEMPERATURE

Among livestock systems, poultry production is probably the one where a strict environmental control has been set up with high requirements, regarding feeding, lighting, temperature, and health. Temperature deserves special consideration for two reasons: poultry production is particularly growing in countries with tropical climatic conditions and heat waves are affecting production in temperate countries, leading to mortality. High economic losses due to heat stress has been documented since many years for livestock production (St Pierre *et al.*, 2003). Highly producing animals are more sensitive to high temperature conditions mainly because they need to dissipate metabolic heat associated to protein synthesis. Of course, performance of selected lines remain higher than that of local unselected populations, but this corresponds to what is called ‘yield gap’ in plant production, where the observed performance does not match the expected genetic gain. Thus, chronic heat stress is setting a limit to the expression of response to selection.

Genetic solutions to improve heat tolerance have been proposed with major genes decreasing feather cover, such as the Naked neck gene and more recently the scaleless gene (Cahaner *et al.*, 2008). Yet, there is little adoption of these solutions until now, probably because introducing a major gene or replacing a line by another one is much more complex than changing a selection coefficient or introducing a new trait in a line. Furthermore, the fully naked scaleless chickens was not appealing for consumers. Thus, research is still active in looking for selection criteria that would improve heat tolerance in chickens, but there may be a biological limit in dissipating metabolic heat.

##### 4.2. ENVIRONMENTAL FACTORS AS A LIMIT TO OVERALL POULTRY PRODUCTION

As compared to ruminants, poultry can be considered to be on the safe side from the viewpoint of Green-House-Gas production, thanks to the high feed efficiency of commercial lines. Another currently active debate relates to the use of high quality feed for animals, such as soybean and corn, which can also be used directly for human nutrition, and occupy arable lands that could be used to produce other vegetal proteins for human nutrition. Thus, a potential competition between poultry feed and human food can be seen here, and a land-use approach has been proposed to analyze the contribution of animal products to sustainable diets (Van Zanten *et al.*, 2016). With such an approach, animal proteins from grazing systems are favored. A model has been proposed to define the optimal proportion of animal protein in human diets, depending on human population size and on the relative share of land unsuitable for crop production (Van Kernebeek *et al.*, 2016). It showed that land was used more efficiently when the proportion of animal proteins in the diet ranged from 15% to 45% for large human populations. Unfortunately, the case of poultry production was not tested in these studies which dealt with cattle and sometimes pig.

Whereas the land use approach of sustainable food systems does not directly set a limit to selection response, it sets a new framework to define selection objectives in poultry. Since breeders and producers are already aware of this debate, diversification of feed resources has been considered. As an example, genetic variability of digestibility has been studied in the case of sup-optimal diets made of wheat, and selection for apparent metabolizable energy corrected for zero nitrogen balance (AMEn) has been shown to decrease environmental impact in broilers (De Verdal *et al.*, 2013). Yet, suboptimal diets may be used at the production level that differ from the diet used for the selection nucleus. This may lead to an environmental limitation to selection response, on the same model as the yield gap, where observed performance stays behind genetic trend.

#### 5. STRATEGIES TO OVERCOME LIMITS

##### 5.1 REFINING BIRD MANAGEMENT OR BREEDING METHODS

###### -Management

Feed restriction is one example of an efficient management solution to the problem of low reproduction in broiler breeders, but it raises a welfare issue.

Cooling devices and nutritional strategies have also been developed to alleviate heat stress. Air conditioning is raising an issue of power supply, and even an ethical issue, since in some countries chickens would be housed in better temperature conditions than humans..., in order to feed humans, from the same country or other countries.

Tailored nutritional approaches have also been proposed for broilers (Gous and Morris, 2005), but limitation of performance due to heat stress remains an issue.

Refining management is generally the best solution on a short-term basis, but may not be sufficient on the long term.

###### -Breeding methods

###### -Adding a new selection criteria targeting the affected biological pathway

This approach has the advantage of having a cumulative effect. In the case of ascites, the oxygen saturation of arterial blood has been suggested to be a promising selection criterion according to Navarro *et al.*, (2006), whereas other studies questioned the efficiency of this measure because of its low heritability (Druyan *et al.*, 2007; Closter *et al.*, 2009).

###### -Improving the selection method

A major progress has occurred with the introduction of genomic selection, which takes advantage of using a high number of SNP markers over the whole genome in order to obtain a genomic prediction of the breeding value, more accurate than the one based on pedigree relationships. It requires genotyping and phenotyping a reference population and can be particularly interesting to estimate breeding values

of males for female traits as well as breeding values of a young animal for an adult trait. Poultry breeders have now adopted this method and it has been suggested to be a suitable approach to improve welfare by applying group selection to select against cannibalistic behavior (Alemu *et al.*, 2016). A more efficient selection method opens new opportunities to implement a revision of selection objectives. Yet, the most powerful the breeding methods become, the most responsible the breeders must be regarding society. Defining selection objectives must take into account the contribution of poultry to the whole agricultural and food systems.

These strategies lead to an increased complexity of breeding programs and production systems, with new traits being added into the program. This is decreasing the selection pressure on the other traits and hence slowing their change. At the opposite, decreasing selection pressure on growth rate would release additional selection intensity for new traits such as disease resistance or behavior.

## 5.2 ALTERNATIVE GENOTYPES AND REVIVAL OF LOCAL BREEDS

In France, the Label Rouge chicken combines a specific production system with a slow-growing genotype, and has been recognized by a specific regulation in 1965 ([www.synalaf.com](http://www.synalaf.com)). Birds cannot be slaughtered before the age of 84 days at a live weight varying between 2 and 2.5 kgs. This performance level is similar to the one of the Athens-Canadian randombred population studied by Havenstein *et al.*, (2003) as a representative of the broiler of 1957. It also matches quite well with the ‘Chicken of Tomorrow’ from The Netherlands, which represents an interesting convergence between countries at two different time frames. Diet of Label Rouge chickens has to include only plant products, even before the mad cow disease. Housing generally includes an outdoor space and a lower bird density that for fast-growing broilers. Meat quality defects are not reported as a major issue as it is standard broilers. Yet, these birds could express more stress at slaughter, probably because they are more active than fast-growing broilers. The Label Rouge system is well accepted by consumers because they consider it as less industrial and more natural, with both sexes being marketed. Yet, it is more costly because birds have a longer life span and eat more for their maintenance requirements than their production requirements. So, their environmental impact is higher for this reason. The outdoor option represents a sanitary risk, which becomes a critical issue in the case of avian influenza that can be transmitted to humans.

Growth rate of local breeds is below the one of Label Rouge in France, but the meat is generally very much appreciated. Successful niche markets have developed for some of them, thanks to the attribution of a quality sign, such as PDO in Europe (AOC in France). The Bresse chicken is an emblematic example of this alternative system, which was officially recognized in 1957 and is still successful, with a range of 1,000,000 chickens produced each year. As reported by Verrier *et al.*, (2005), this production requires a specific coordination mechanism between farmers and the manager of the breeding nucleus (Centre de Sélection de Béchanne, CSB). Birds are also individually tagged to build trust with the consumer. Close relationships with famous French cooks is used to promote the breed as a high-quality product. This system has saved this breed and has maintained a traditional farming system, with a typical finishing period using milk and bread crumbs. Other local breeds in France have tried to follow this example, but getting a PDO is hard and, until now, no other breed got it, but some of them use trademarks to differentiate them from others. Their organization is generally local with an association working with the CSB to set up a secure nucleus of their breed, from the viewpoint of genetic as well as sanitary management. Maintaining a collective organization is key to the sustainability of these initiatives (Tixier-Boichard *et al.*, 2006). As a result, the number of French chicken local breeds involved in a small production system with a sustainable management of their genetic diversity ranges around 20. The link to a specific environment is difficult to establish in poultry but more diversified diets can be used, as compared to the Label Rouge which still relies mainly on corn/soybean diets. Yet, none success story is known for egg production, probably because the production cycle is even longer and it is more difficult to distinguish a ‘local egg’ from a standard egg in the plate. Egg diversification has been much more influenced by the perception of production system (cages/floor) and the development of organic egg production.

The Spanish ministry of agriculture has undertaken a different labelling approach to support local breeds by defining the “raza autoctona” brand applicable to all of them, so that there is no competition between local breeds and it promotes a global support to genetic diversity.

The main limitation of these systems stands at the economic level. Because of the high production costs of a slow growing chicken, the price for the consumer is higher by more than 50% for Label Rouge and it is multiplied by 2.5 or more for the Bresse. Thus, these markets remain small but provide a positive image of poultry breeding.

Another option explored by breeding companies is to come back to dual-purpose breeds, which has the advantage of avoiding low fitness due to extreme performance and of solving the issue of male day-old chicks in layers. At present, dual-purpose birds are often derived from crosses, which is more simple to set up than to start a new selection program. Their production cost is of course higher than the one of high-performing broilers or layers but their growth rate is intermediate between standard broilers and Label Rouge broilers and they exhibit a better welfare according to a German study reported by Poultry World (<https://www.poultryworld.net/Genetics/Articles/2019/6/What->

**Table 1: comparison of high-performing broilers, Label Rouge broilers, local breeds such as Bresse, and dual-purpose chickens, for their sensitivity to limits (1: little affected; 2: moderately affected; 3: strongly affected)**

|                 | Biological/fitness | Ethics | Environment | Economic efficiency |
|-----------------|--------------------|--------|-------------|---------------------|
| Genotype        |                    |        |             |                     |
| High-performing | 3                  | 3      | 3           | 1                   |
| Label Rouge     | 1                  | 1      | 2           | 2                   |
| Bresse          | 1                  | 1      | 1           | 3                   |
| Dual-purpose    | 1                  | 1      | 2           | 2                   |

role-for-the-dual-purpose-chicken-434396E/?cmpid=NLC|pigprogress|2019-07-11|What\_role\_for\_the\_dual-purpose\_chicken).

These different genotypes are tentatively ranked for their sensitivity to different limits in Table 1.

Obviously, there is not a one-for-all genotype. Depending on the weight given to the different component of possible limits, the best genotype will vary. At present, economic efficiency gets the highest weight, so that high-performing lines get the largest market share, but sustainable development calls for a more balanced weighting of these components.

FAO is promoting a transition to sustainable food and agricultural systems relying on agroecology (<http://www.fao.org/about/meetings/second-international-agroecology-symposium>). Maintaining a choice of genotypes, for adaptation to a variety of production environments and market needs, is a breeding strategy suited to agroecology (Phocas *et al.*, 2016). The choice may include different commercial lines, but also alternative genotypes such as the slow-growing broiler, and different crossbreeding combinations.

### 5.3 PRESERVATION OF GENETIC DIVERSITY AND GENE BANKS

Maintaining genetic variation is a key for adapting breeding strategies. To avoid the limitation due to low genetic variation, maintaining genetic reserve, either in vivo or in vitro (i.e. gene banks) offers the possibility to renew the genetic basis of a breeding program by using crossbreeding and/or deriving new composite populations. Research has made progress on cryopreservation of sperm and more recently of primordial germ cells in order to improve efficiency of use of gene bank materials.

Moreover, the overall gene pool of chickens is still high if we consider all local populations, and the wild ancestor species is still existing, which should be viewed as a great opportunity to enlarge the choice of genotypes in gene banks as well as in the field, since gene banks are a necessary support to live genetic diversity.

## Conclusions

The occurrence of a true selection plateau has not been observed yet, which could be due to the relatively short duration of selection, from an evolutionary viewpoint. Yet, the selection of extreme phenotypes leads to biological limits due to unfavorable correlated responses. Research is working to propose solutions to go beyond these limits, but the current situation of meat quality defects, as an example, has not yet found a solution that would not affect growth rate at the same time.

The more critical sources of limits to selection on poultry are ethical and environmental, because solutions to overcome them lead to reconsider the whole system. The main challenge is now to establish more balanced selection objectives, targeting optimal performance rather than maximal values in order to meet the expectation of sustainable food systems for human societies.

Whereas poultry breeding has always been very reactive to market trend, it must take care of preserving a diversity of genotypes to better take into account wider concerns about environmental limits in order to promote a sustainable use of resources by animal production.

## References

- ALEMU, S.W., CALUS, M.P.L., MUIR, W.M., PEETERS, K., VEREIJKEN, A. and BIJMA, P. (2016) Genomic prediction of survival time in a population of brown laying hens showing cannibalistic behavior *Genetics, Selection, Evolution* 48: 68.
- CAHANER, A., AJUH, J.A. SIEGMUND-SCHULTZE, M., AZOULAY, Y., DRUYAN, S. and ZARATE, A.V. (2008). Effects of the genetically reduced feather coverage in naked neck and featherless broilers on their performance under hot conditions. *Poultry Science* 87: 2517-2527.
- CLOSTER, A.M., VAN AS, P., GROENEN, M.A.M., VERIJKEN, A.L.J., VAN ARENDONK, J.A.M. and BOVENHUIS, H. (2009) Genetic and phenotypic relationships between blood gas parameters and ascites-related traits in broilers. *Poultry Science* 88: 483-490.
- DE VERDAL, H., MIGNON-GRASTEAU, S., BASTIANELLI, D., MÊME, N., LE BIHAN-DUVAL, E. and NARCY, A. (2013) Reducing the environmental impact of poultry breeding by genetic selection. *Journal of Animal Science* 91: 613-622.
- DERKS, M.F.L., MEGENS, H.J., BOSSE, M., VISSCHER, J., PEETERS, K., BINK, M.C.A.M., VEREIJKEN, A., GROSS, C., DE RIDDER, D., REINDERS, M.J.T. and GROENEN, M.A.M. (2018). A survey of functional genomic variation in domesticated chickens. *Genetics, Selection, Evolution* 50: 17.
- DRUYAN, Z., SHLOSBERG, A. and CAHANER, A. (2007) Evaluation of growth rate, body weight, heart rate, and blood parameters as potential indicators for selection against susceptibility to the ascites syndrome in young broilers. *Poultry Science* 86: 621-629.
- DUNNINGTON, E.A., HONAKER, C.F., MCGILLIARD, M.L. and SIEGEL, P.B. (2013). Phenotypic responses of chickens to long-term, bidirectional selection for juvenile body weight- Historical perspective. *Poultry Science* 92: 1724-1734.
- ELSON, H.A. (2014). Poultry welfare in different production systems. In *Proceedings of the XIVth European Poultry Conference*, Stavanger, Norway, June 23-26, 2014, pages 251-259. WPSA
- GOUS, R.M. and MORRIS, T.R (2005) Nutritional interventions in alleviating the effects of high temperatures in broiler production. *World's Poultry Science Journal* 61: 463-475.
- GRANEVITZE, Z., HILLEL, J., CHEN, G.H., CUC, N.T.K., FELDMAN, M., EDING, H. and WEIGEND, S. (2007) Genetic diversity within chicken populations from different continents and management histories. *Animal Genetics* 38: 576-583.
- HARDIN, E., CASTRO, F. L. S. and KIM, W. K. (2019) Keel bone injury in laying hens: the prevalence of injuries in relation to different housing systems, implications, and potential solutions. *World's Poultry Science Journal* 75: 285-291.
- HAVENSTEIN, G. B., FERKET, P.R. and QURESHI, M.A. (2003) Growth, livability, and feed conversion of 1957 versus 2011 broilers when fed representative 1957 and 2011 broiler diets. *Poultry Science* 82: 1500-1508.
- HILL, W.G. and KIRKPATRICK, M. (2010). What animal breeding has taught us about evolution. *Annual Review of Ecology, Evolution, and Systematics* 41: 1-19.
- MALOMANE, D.K., SIMIANER, H., WEIGEND, A., REIMER, C., SCHMITT, A.O. and WEIGEND, S. (2019) The SYNBREED chicken diversity panel: a global resource to assess chicken diversity at high genomic resolution. *BMC Genomics* 20: 345.

- MARKS, H.L. (1996) Long-term selection for body weight in Japanese quail under different environments. *Poultry Science* 75: 1198-1203.
- MIGNON-GRASTEAU, S., BEAUMONT, C. and RICARD, F.H. (2001) Genetic analysis of a selection experiment on the growth curve of chickens. *Poultry Science* 80: 849-854.
- NAVARRO, P., VISSCHER, P. M., CHATZIPLIS, D., KOERHUIS, A. N. and HALEY, C. S. (2006) Genetic parameters for blood oxygen saturation, body weight and breast conformation in 4 meat-type chicken lines. *British Poultry Science* 47: 659-670.
- PETRACCI, M., SOGLIA, F., MADRUGA, M., CARVALHO, L., IDA, E. and ESTEVEZ, M. (2019) Wooden-breast, white striping, and spaghetti meat: causes, consequences and consumer perception of emerging broiler meat abnormalities. *Comprehensive Reviews in Food Science and Food Safety* 18: 565-583.
- PHOCAS, F., BELLOC, C., BIDANEL, J., DELABY, L., DOURMAD, J. Y., DUMONT, B., EZANNO, P., FORTUN-LAMOTHE, L., FOUCRAS, G., FRAPPAT, B., GONZALEZ-GARCIA, E., HAZARD, D., LARZUL, C., LUBAC, S., MIGNON-GRASTEAU, S., MORENO, C. R., TIXIER-BOICHARD, M. and BROCHARD M. (2016) Review: Towards the agroecological management of ruminants, pigs and poultry through the development of sustainable breeding programmes: II- Breeding strategies. *Animal* 10: 1760-1769.
- ROBERTSON, A. (1960) A theory of limits in artificial selection. *Proceeding Royal Society of London. Ser. B* 153: 234-249.
- ST-PIERRE, N.R., COBANOV, B. and SCHNITKEY, G. (2003) Economic losses from heat stress by US livestock industries. *Journal of Dairy Science* 86: E52-E77 (Suppl.)
- TIXIER-BOICHARD, M., AUDIOT A., BERNIGAUD R., ROGNON X., BERTHOULY C., MAGDELAINE P., COQUERELLE G., GRINAND R., BOULAY M., RAMANANTSEHENO D., AMIGUES Y., LEGROS H., GUINTARD C., LOSSOUARN J. and VERRIER E. (2006) Valorisation des races anciennes de poulets : facteurs sociaux, technico-économiques, génétiques et règlementaires. *Les Actes du BRG*, 6: 495-520.
- VAARST, M. (2014). Sustainable development perspectives of poultry production. Plenary conference. In *Proceedings of the XIVth European Poultry Conference*, Stavanger, Norway, June 23-26, 2014, pages 55-66, WPSA.
- VAN KERNEBEEK, H.R.J., OOSTING, S.J., VAN ITTERSUM, M.K., BIKKER, P. and DE BOER I.J.M (2016) Saving land to feed a growing population: consequences for consumption of crop and livestock products. *International Journal of Life Cycle Assessment* 21: 677-687.
- VAN ZANTEN, H.H.E., MEERBURG, B.G., BIKKER, P., HERRERO, M. and DE BOER, I.J.M. (2016) Opinion paper: the role of livestock in a sustainable diet: a land-use perspective. *Animal*, 10: 547-549.
- VERRIER, E., TIXIER-BOICHARD, M., BERNIGAUD, R. and NAVES, M. (2005) Conservation and values of local livestock breeds: usefulness of niche products and/or adaptation to specific environments. *Animal Genetic Resources Information*, 36: 21-31.
- WADE, M.J., BIJMA, P., ELLEN, E.D. and MUIR, W. (2010) Group selection and social evolution in domesticated animals. *Evolutionary applications*, 3: 453-465.
- WIDEMAN, R. F., RHOADS, D. D., ERF G. F. and ANTHONY, N.B. (2013) Pulmonary arterial hypertension (ascites syndrome) in broilers: A review. *Poultry Science*, 92: 64-83.
- ZHAO, X.L., HONAKER, C.F. and SIEGEL, P.B. (2012) Phenotypic responses of chickens to long-term selection for high and low antibody titers to sheep red blood cells. *Poultry Science*, 91: 1047-1056.