Slov Vet Res 2013; 50 (3): 139 - 44
UDC 636.5.082:575.2

Review Article

DIVERGENT SELECTION EXPERIMENTS IN POULTRY

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Summary: The importance of quantitative genetics is obvious for poultry breeders as most traits of economic value are quantitative. To better understand quantitative traits, much research has been conducted using short- and long-term divergent selection experiments in chickens and quails over the last decades. In the past, divergent selection experiments were conducted for a variety of reasons such as estimating genetic parameters, testing alternate breeding schemes, measuring selection limits and plateaus, testing theoretical basis relating population sizes and selection intensities, searching for correlated responses to selection on a focal trait, ascertaining the symmetry of responses in a particular trait, etc. Genetically correlated traits are known to respond to indirect selection pressures caused by directional selection on other traits. Thus correlations are of great interest to the breeders. Additionally, information on genetic correlations between traits may provide insight into the biological mechanisms involved in generating differences between selection lines. Divergent selection experiments resulted in a wealth of unique populations of chickens/quails that are very useful for subsequent biochemical or physiological studies, and for studying of genotype by environment (GxE) interactions. GxE interactions are of fundamental importance in poultry breeding because their involvement influences breeding procedure. Geneticists have long been concerned with identifying key genes responsible for variation in quantitative traits. Intercrosses between divergently selected chicken/quail lines have led to the identification of several quantitative trait loci affecting for growth, egg production and quality, feed consumption, disease resistance and other traits.

Key words: poultry; divergent selection; correlated responses; quantitative trait loci

Introduction

With the rise of genetics as a field of science in the 1920's and 1930's, artificial selection experiments became a standard tool in quantitative genetic research. They have been and continue to be a powerful tool to yield information on quantitative traits in terms of their underlying genetic variability, the relationships between traits and their effects on performance (fitness). In addition, selection experiments have provided stocks that have been useful for many other topics, from estimating mutation rates to understanding the molecular, biochemical, and physiological foundations of trait variation (1, 2). Several designs of selection experiments can be distinguished: selection may be practiced in a single direction without a control population, or, control can be maintained to remove environmental variation over generations. In an alternative design, such as divergent selection, the selection is practiced in two lines in opposite directions for the same trait and the difference in performance between the lines is recorded. Common environmental effects are again eliminated (3). This paper briefly reviews poultry divergent selection experiments and some of the results obtained to discuss aspects of

Received: 4 January 2013
Accepted for publication: 22 February 2013

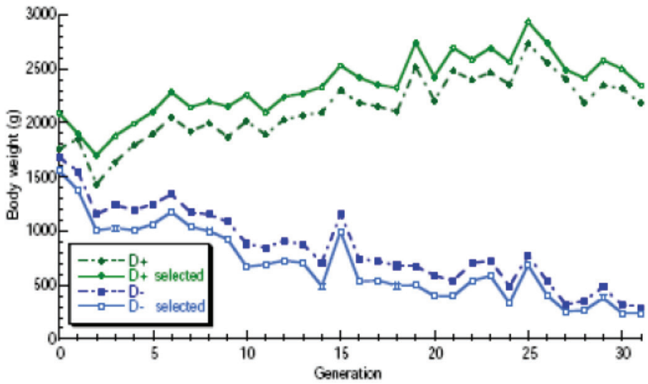

Figure 1: Response to selection for high (D+) and low (D-) 8-wk weight (»selected«=chickens selected to be parents of the next generation). In the photo, both, the low and high weight line birds, are of selection age, where they show almost an eight-fold weight difference (10).

selection experiments that should be considered for the continuation of existing experiments or before future poultry selection experiments are established.

Divergent selection experiments

The motivation to apply divergent selection on quantitative characters was the following (4): a) to demonstrate the principles of quantitative genetics; b) to test for possible departures from predictions; c) to investigate the long-term responses and selection limits; d) to establish differentiated populations for further genetic, physiological or nutritional studies; e) to estimate genetic parameters such as heritabilities; f) to investigate changes in other traits which may be correlated; g) to compare alternative selection schemes. Selection experiments may be viewed in the short- and long-term. Evolutionary biologists, especially quantitative geneticists, are usually interested in the long-term response to selection, which is usefully considered in terms of fixation probabilities of alleles underlying the trait(s) under selection. Over the short term (a few generations), the response to selection will primarily be a function of the alleles segregating in the base population (5). More than 30 generations of selection might be needed to accomplish most of the goals of long-term selection experiments (6). In classical selection experiments, chickens (layers, broilers) and quails can serve as good models for several reasons. They are fairly easy and relatively cheap to maintain in larger numbers, they produce comparatively large numbers of offspring and many interesting characteristics are easy to score (body weight-BW, plumage colour, body composition, metabolic and immunological traits, etc.). This, in addition to a short generation time and high recombination rate, renders chickens and quails suitable as models for genetic studies (7, 8).

Selection traits

The majority of divergent selection experiments in poultry can be grouped according to the selection objectives of either growth and carcass traits, or, various physiological, endocrinological, nutritional, immunological, behavioral, and molecular traits. Several selection experiments are presented in Table 1. Single trait long-term selection experiments with closed populations provide information that cannot be obtained from multitrait selection experiments or from analyses of commercial breeding programs where introgression may occur (9). Because of that, the bulk of studies carried out in poultry have been single-trait selection experiments. Terčič and Holcman (10) (Figure 1) as well as Dunnington and Siegel (11) have summarized the results from an unprecedented and classical long-term selection experiments of 31 and 38 generations, respectively. In both experiments, the common founder populations originated from meat-type crosses. The two lines have been maintained as closed populations selected for either high or low BW at 8 weeks (wk) of age. Various aspects of direct and correlated effects of selection for BW were investigated in depth to understand the mechanisms of selection at organismal, cellular, and molecular levels (10, 11). Different lines (selected, relaxed, dwarf) and line crosses proved to be excellent models for the study of long-term effects of selection for growth (6).

The majority of studies have one selection objective, but few studies have several selection objectives for direct comparison of selection

Table 1: Selection objectives, experimental designs and duration of several selection experiments in chickens

Selection objective	Design[1]	Generations of selection / Reference
8-wk BW	D	16 / (12) ; 31 / (10)
8-wk BW	D+C	38 / (11)
proportion of abdominal fat	D	7 / (13)
residual feed consumption	D	15, 18 / (14)
apparent metabolisable energy corrected for zero nitrogen balance	D	8 / 15
responsiveness to photoperiod	D	4 / (16)
large and small yolk proportions	D	1 / (17)
feather pecking behaviour	D+C	5 / (18)
resistance to Rous sarcoma virus	D	18 / (19)
immune response in chickens	D+C	18 /(20)
ascites incidence	D+C	10 / (21)
serum immunoglobulin levels		3 / (22)
exponential growth rate to 14 or 42 days of age	D	5 / (23)
incidence of tibial dyschondroplasia	D+C	10 / (24)
phytate phosphorus bioavailability	D	3 / (25)

[1]Divergent selection with (D + C) or without (D) a control

strategies. Inclusion of two selection objectives enables measurement of the direct response in trait X, the correlated response in trait Y, and vice versa, in the complementary selection lines, and permits testing of predicted and realised responses to selection (26). For example, divergent selection in generations 10 to 13 of Japanese quail for either 4-week BW or for laying hen yolk precursor (indirectly by increased total plasma phosphorus-HP, decreased total plasma phosphorus-LP) for improvement the shell characteristics, has enabled direct comparison of the selection strategies (27). Selection for several objectives may be more informative than selection for only one objective. To determine correlated responses between growth at different ages and body composition, chickens were divergently selected for exponential growth rate (EGR) to 14 or 42 days of age over five generations (23). During the selection experiment, selection for fast EGR14 or EGR42 increased fat at the age of selection. However, selection for fast EGR42 increased BW and percentage fat at 42 d of age, whereas selection for fast EGR14 increased BW but not fat at 42 d of age (23). Several studies have selected on a correlated trait, rather than on the trait of interest. Divergent selection for serum immunoglobulin M and G levels in chickens changed antibody producing cells as well as other immunocompetent cells that modulate the immune response of the selected lines (22). Divergent selection for total plasma phosphorus in Japanese quail was applied in order to reduce the fearfulness as measured by tonic immobility and consequently to reduce the mortality (28).

Correlated responses

The selection experiment provides an effective resource to estimate genetic covariances with traits in the selection criterion, particularly for traits which are either difficult or expensive to measure (26). For instance, a selection on feed efficiency of laying hens, independent of BW and egg production, requires controlling feed consumption on an individual, or at least on a family basis. This control is costly in time and money. Also, it may be difficult to provide an environment, where genetic improvement is desired. For instance, in selection for resistance to a specific disease because of the cost and risks of exposure (29). In the 1980's, chicken lines were developed that are either high or low in antibody (Ab) production against sheep red blood cells (SRBC). The ultimate goal of developing such lines is to improve some immune parameters, and hence improve resistance to specific diseases (30). Many chickens remain contaminated by

Salmonella for several weeks without showing any symptoms (asymptomatic carriers). Since these healthy carriers are an obstacle to the eradication of Salmonella, selection for increased resistance to Salmonella carrier state could improve both, animal health and food safety. INRA researchers in France have developed two series of divergently selected lines for either low or high carrier state resistance in both, young chicks and adult hens (31). Genetic relationships between carcass composition with meat and eating quality traits are required for the effective inclusion of meat and eating quality traits in breeding programmes and ultimately for the evaluation of alternative selection strategies (26). Many studies showed that inosine-5′-monophosphate (IMP) and intramuscular fat (IMF) contribute to the sensory perception of meat delicacy. From the experiment, where chickens derived from the first two generations of divergent selection for the percentage of IMF and selection for increased IMP content in breast meat were used, it was concluded that both, IMP and IMF contents in chicken meat, have the potential to be increased through genetic selection with little or no positive effect on BW (32). Over the past decade, there has been a highly increased interest in breeding to improve chicken feed efficiency. However, the biological basis of variation in feed efficiency is yet to be fully understood. To examine the biological mechanisms underlying feed efficiency in laying hens, a divergent selection for residual feed intake was started in 1976 (33).

Analysis of genotype-by-environment interaction

The term »genotype-G x environment-E interaction« is most commonly used to describe situations where different genotypes (for instance divergently selected lines) respond differently to different nutritional/climatic environments (34). The importance of GxE interactions to both, the poultry breeder and the poultry producer, appears to be in the choice of performance testing regime in nucleus stocks, to take account of the regime in which commercial animals are reared. Many studies on GxE interactions have been reported for chickens. One cycle of divergent selection for abdominal fat was performed in broilers raised under three different climatic conditions (35). The difference between the high-fat (HF) and low-fat (LF) selection lines had the same magnitude under different environmental conditions that increase or decrease fat deposition. Growth rate (GR) and meat yield depression have been more pronounced in meat-type chicken genotypes (lines) with higher BW and more rapid GR than in those with lower BW and GR (36).

Quantitative trait loci

A powerful way to examine the genetic control of trait variation is to use quantitative trait locus (QTL) analysis, which examines, statistically, the phenotypic effects associated with genetic regions that are delimited by molecular markers (5). Divergently selected lines of chickens for BW, abdominal fatness, immune response, and other traits are frequently used to create marker populations with high amounts of genetic variation for QTL analysis. Calenge et al. (31) used commercial laying hen lines divergently selected for resistance to Salmonella carrier state at two different ages to identify several QTL carrier state resistance variations. Interestingly, previously identified QTL for resistance to carrier state in a chicken F2 experimental population were also validated in divergently selected lines. Simulation studies demonstrated the usefulness of rearing animals more resistant to carrier state in the prevention of Salmonella disease propagation in poultry, in synergy with vaccination (37). The genetics behind complex traits may be studied by intercrossing divergently selected lines with distinct phenotypic differences. One such cross was generated between two lines of chickens divergently selected for BW at eight weeks of age for 25 generations. Intercross facilitated mapping of loci involved in growth and fatness-related traits (38).

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DVOSMERNI SELEKCIJSKI POSKUSI V PERUTNINARSTVU

D. Terčič

Povzetek: Poznavanje zakonitosti kvantitativne genetike je za selekcijske hiše v perutninarstvu zelo pomembno, saj je večina gospodarsko pomembnih lastnosti kvantitativnih. Zaradi boljšega razumevanja omenjenih lastnosti je bilo v zadnjih desetletjih na kokoših in prepelicah izpeljanih veliko kratkotrajnih in dolgotrajnih dvosmernih selekcijskih poskusov. Njihov namen je bil večkraten: ocena genetskih parametrov, testiranje možnih načinov rej živali, merjenje skrajnih selekcijskih meja, testiranje teoretičnih modelov povezanih z velikostmi populacij in intenzivnostmi selekcije, iskanje koreliranih in ugotavljanje asimetričnih učinkov selekcije, itn. Za genetsko korelirane lastnosti je znano, da je mogoče nanje vplivati posredno z neposredno selekcijo na ostale lastnosti. Zato je za selekcioniste poznavanje korelacij velikega pomena. Dodatno lahko poznavanje genetskih korelacij ponudi vpogled v biološke mehanizme, ki povzročajo razlike med selekcijskimi linijami. Dvosmerno selekcionirane linije kokoši/prepelic so dragocen material za naknadno izvajanje biokemijskih in fizioloških raziskav ter za študij interakcij med genotipom in dejavniki okolja. Ker je od interakcij med genotipom in okoljskimi dejavniki odvisna izbira okolja, v katerem bo potekalo testiranje živali, so za selekcioniste v perutninarstvu vitalnega pomena. Genetiki se že vrsto let ukvarjajo z identifikacijo ključnih genov oziroma regij v genomu, ki vplivajo na kvantitativne lastnosti. S križanji med dvosmerno selekcioniranimi linijami kokoši je bilo identificiranih več kvantitativnih lokusov, ki vplivajo na rast, prirejo in kakovost jajc, zauživanje krme, odpornost na bolezni ter na druge lastnosti.

Ključne besede: perutnina; dvosmerna selekcija; korelirane lastnosti; kvantitativni lokusi