1 INTRODUCTION

1.1 Poultry production in Mozambique

In the last decade the increase in poultry meat production was quite similar on all continents, while egg production showed a great variability. During this period, egg production in the developing countries, which include most of the hot regions of the world, increased by 47.2 %, and by only 5.6 % in the developed world. For poultry meat, the difference between developing and developed countries was only 16.6 % (Daghir, 1995). In Africa, although poultry products substantially contribute to the protein intake in most countries, per capita consumption is still low. Adegbola (1988) reported that on average only 44 eggs were produced in the African continent per person per year, while in South Africa the figure is 89 (FAO, 1990). There is no doubt of the need for more eggs and poultry meat in order to fulfil the increasing protein requirements of the African population.

In Mozambique, as in many other African countries, egg and poultry meat are important sources of animal protein. Poultry production systems vary widely from the extensive free-range keeping (scavenging) of very small flocks for self-consumption, to intensive management of medium size or large flocks, mainly for market. In the fringe of the main cities, an increasing peri-urban, semi-intensive and semi-commercial system plays an important role in the supply of poultry products mainly to informal markets. The dualism of the production systems is also reflected in breeding. Local or indigenous breeds, in some cases crossed to an unidentifiable degree with exotic breeds, prevail in the subsistence and semi-commercial systems. In general, their productivity, expressed in terms of egg production and growth rate, is low and survivability is limited due to diseases and predators. However, they are specially adapted to unfavourable climates and extensive management conditions owing to their low metabolic efficiency and their characteristic brooding and maternal ability. Specially selected populations from temperate climates are utilised in intensive meat or egg production systems and to a lesser extent in semi-intensive peri-urban systems. Although performance and liveability can be reduced as a result of the tropical environment, the productivity of such birds is reasonable, provided that the nutritional and managerial inputs match their genetic potential.

For many years after independence, poultry production was run by the state, and the state farms produced around 95 % of the poultry products consumed in 1980. In 1987, with the collapse of the prevailing political system, some of the state farms were privatised and others discontinued. The newly emerging private sector partly replaced the previous state production, so that in 1991 the meat output had declined by 44 % and the egg production by 92 %. In the peri-urban zone of Maputo, poultry meat production in small units of up to 200 broilers per batch, a considerable number of which are owned by women, has largely increased in the last eight years. Day-old chicks, feed and vaccines, which were scarce in the past, are available nowadays. Local production has boomed and contributes to approximately 80% of the estimated consumption, with a large percentage of birds being sold live in peri-urban markets.

The same development trend was not observed in the production of table eggs. In 1982, egg production peaked at 31.5 million but declined to 2.4 million in 1991 (DINAP, 1994). The private sector is by far the main producer, comprising a large number of medium size farms with 100 to 200 layers, while small-scale units of up to 20 layers and large ones with tens of thousands birds, also exist. Private output seems to have reached a plateau at 4.5 million eggs in the last years, although imports are about ten times the local production in Maputo (DINAP, 1998). Possible reasons for the decline in commercial egg production could be: longer production cycles, longer repayment period of loans, lower return on capital and cheaply imported eggs. Climate and genetics are also to be considered. High temperature, especially when associated with high humidity, imposes severe stress on birds, leading to reduced performance of the high-yielding, non-heat-tolerant layer strain locally available.

1.1.1 The prospects for developing the rural poultry sector

The rural poultry production system is mainly based on the scavenging indigenous chickens found in virtually all villages and households throughout the country. These systems are characterised by nil or minimal inputs for housing, feeding or veterinary care and by a low output per bird. The birds are usually maintained as a source of meat, with few eggs being consumed and fewer being sold, and the majority destined for incubation.

Although no official figures are available for Mozambique, the contribution of the sector might be close to 70 % for poultry products and 20 % for animal protein intake as reported by Kitalyi (1998) for most African countries. Therefore, improved rural poultry production would result in a significant impact on the family food security through increased protein intake and income generation.

The potentials, major constraints and possible solutions for improved production have been identified. As a result of the major threat imposed on their flocks by predators and decimating diseases like Newcastle Disease (ND), and in view of the meagre output obtained, the farmers perceive the scavenging chicken as a natural low grade crop, too unreliable to be worth investing any of their scarce resources. As soon as the ND is controlled, the full economic potential of the village chicken and its scavenging environment must be developed, for which a multifaceted approach combining improved management, health, nutrition and breeding is needed.

Attempts to upgrade the local breeds by crossbreeding with males of high producing strains in various countries have not succeeded. One reason is the difficulty the introduced bird has coping with the harsh environmental conditions offered (Adegbola, 1988). As the incubation of eggs by hens markedly reduces the egg supply for consumption, broodiness is an important biological limitation to be overcome once ND is controlled and the farmers have been convinced that husbandry alterations are economically advantageous. A possible integrating approach might be the introduction of a high-yielding layer strain to produce eggs for family consumption and sale, while the incubation and raising of chicks is guaranteed by the village breed, as advocated by Cumming (1992). The revenue from egg sales could help pay for improved feeding of the offspring and thus for increased meat supply.

1.1.2 The prospects for increased peri-urban egg production

Parallel to the significant supply of meat and eggs for the Maputo market, the peri-urban poultry production makes an important contribution to the empowering of women and for the stability of the households thus promoting gender equity. Both the need and the

potential for increase are still great, despite the threat imposed by cheaper imports. As significant investment in large-scale commercial farms is unlikely to occur, the prospects for increasing egg output probably depend on the so-called informal sector. Egg production in small backyard enterprises of up to 30 layers might be easily encouraged and micro-credit, extension services and marketing assistance could be provided to the households, under a scheme similar to the successful one existing for broilers and vegetables.

The economic feasibility of such peri-urban production systems is greatly dependent on the margin over feed costs and the return on capital invested. Eggs produced locally are not graded and the feed price to egg price ratio is relatively high. In these circumstances, a smaller hen like the dwarf could be advantageous, given the reduced space requirements and the lower feed requirements. In peri-urban markets there is a great demand for naked neck and frizzle birds, used for traditional healing ceremonies, and the price relation of these birds to the normal feathered type can be as high as 1.5:1 and 3:1, respectively. A bird carrying such major genes might provide a further economic benefit. The majority of the peri-urban producers are not specialised, producing both eggs and meat from their poultry with an appreciable percentage of the output destined for self-consumption. Thus, a dual-purpose stock, producing both a high yielding layer and a male for meat, could be valuable for backyard semi-commercial production.

1.2 Strategies for poultry development in tropical countries

In the tropics, poultry production is influenced by direct and indirect adverse effects of heat stress. The ability of birds to dissipate their body heat is reduced, feed consumption is depressed and they are unable to maintain optimal reproductive and productive functions. Appropriate management, including mainly housing and feeding techniques can partially compensate for some of the depressing effects of higher temperatures. In addition, breeding and selection programmes can be adopted in order to achieve the best possible results in such unfavourable environmental conditions.

Commercial stocks developed in temperate climates might not achieve optimal performance under the high temperature and humidity conditions of this region of the world. The genotypes of broilers and layers used in the poultry industry changed considerably in the last decades. Genetic improvements have been directed towards a specialist bird, rather than the dual-purpose breeds that were common three decades ago, making it less adequate either for cross-breeding with indigenous breeds or for extensive or semi-intensive production. Strains that are more tolerant of high temperatures and have all the other economic characteristics should be more profitable under the environmental, social and economic conditions of a tropical developing country. Tropical- oriented breeding activities are limited.

An important concept for genetic improvement of tropical poultry populations is based on the «body size x adaptability» phenomenon (Horst & Petersen, 1975; Mathur & Horst, 1989), with both characteristics being negatively correlated. A beneficial side-effect of this concept consists of a reduction of feed cost for maintenance, leading to an improved feed conversion rate for meat and egg production. Under unfavourable climatic conditions and in a situation of scarce resources for animal nutrition, the genetic potential to reduce body size and improve feed efficiency seems relevant. Another important adaptation can be achieved by changing the bird's loss of excessive heat through morphological changes in feathering density and feather structure (Horst, 1981). Regarding breeding strategies, it is very useful that only a few, mainly major gene effects, influence most of these characteristics. This fact allows for the transfer of these tropically relevant genes to high yielding populations by conventional breeding methods, thus improving biological as well as economical adaptation very effectively (Horst, 1989).

1.2.1 Major genes that affect heat tolerance

Major genes of actual breeding interest are those that can improve feed intake and productivity under heat stress, resulting from a more efficient thermo-regulation due to a lower basic metabolism and reduced feathering intensity. There are several genes that affect heat tolerance. The naked neck (*Na*) reduces feather cover, the frizzle (*F*) causes

the contour feathers to curve outward away from the body, and the dwarf (*dw*) reduces body size and thereby reduces metabolic heat output.

Naked neck (*Na*)

This is an incompletely dominant autosomal gene that not only defeathers the neck, but also reduces body feathering by 20-30 % in the heterozygous (*Nana*) and up to 40 % in the homozygous (*NaNa*) genotype. In egg-type birds tested at higher temperatures, the *Na* gene improves heat tolerance as indicated by higher egg production, better feed efficiency, earlier sexual maturity, larger eggs, and lower mortality when compared with normally feathered birds with similar genetic backgrounds. Also, the *Na* gene improves persistency especially in the final stages of the laying period (Rauen *et al.*, 1986). Embryonic losses are 9 % higher in naked neck chicks compared with normal feathered birds, which is compensated by their higher liveability (Mérat, 1990).

Positive effects of this gene on broiler stocks, such as increased carcass weight and meat yield, higher body weights, lower fat content and better feed efficiency have also been reported (Mérat, 1986; Cahaner *et al.*, 1993). Eberhart & Washburn (1993) demonstrated that the *Na* gene conferred resistance to chronic heat stress in an F_2 broiler population of large body weight. There is a significant gene x breed interaction, the positive effect of the *Na* gene being more pronounced in large body sized birds. This provides an advantage in tropical countries where medium heavy dual-purpose birds producing brown-shelled eggs are preferred. Furthermore, results suggest that the advantage of the *Na* gene is more clearly expressed under unfavourable conditions with higher temperatures, smaller diurnal or seasonal fluctuations, and poor management (Horst, 1988; Mérat, 1990).

Frizzle (*F*)

This is also an incompletely dominant autosomal gene that causes the curling of feathers. In homozygous birds, the curving is so pronounced that no feather has a flat vane, with heterozygous showing less extreme effects (Somes, 1990). The frizzle gene reduces the insulating properties of the feather cover (reduces feather weight) making it easier for the bird to radiate heat from the body. Under permanent heat stress, the *F* gene improves the

productive adaptability of laying hens, leading to superior egg number, egg mass and feed efficiency, although the single effect of the *F* gene is inferior to that of the *Na* gene (Mathur & Horst, 1992; Haaren-Kiso *et al.*, 1994). There is evidence indicating that this gene may be useful in stocks that have to perform under hot humid conditions (Gowe & Fairfull, 1995).

Dwarf (*dw*)

This is a sex-linked recessive gene and is associated with reduction of body weight of the homozygous males by about 43 % and that of homozygous females by approximately 30 %. The gene causes a reduction of egg weight up to 10 % and egg number up to 7 %. In general, disadvantageous effects on egg weight and number of eggs produced are less pronounced in heavier genotypes as brown egg layers, or broiler breeders. Dwarf hens show a slight delay on sexual maturity, and reduction of sequence length. Their body maintenance requirements are lower than large-bodied birds, and since their egg mass relative to body weight is greater, feed efficiency is significantly higher (up to 25 %). Furthermore, the dwarf gene is also associated with an increased number of hatching eggs and significantly higher liveability. Cracked and abnormal eggs from dwarf layers are reduced by up to 80 % (Renden & McDaniel, 1984; Mérat & Bordas, 1991).

1.2.2 Use of major genes in breeding for resistance to heat stress

The *Na* gene can be successfully incorporated by back-crossing into high performing meat or egg laying stocks. If the gene can be obtained in a stock already improved, fewer back-cross generations will be required (Horst, 1989). The evidence available suggests that the *F* gene can be used along with the *Na* gene to develop stocks specially for the hot and humid climates, since these genes can interact to improve the performance of layers under heat stress (Horst & Mathur, 1994). The combined effects of both genes are lower than the sum of their individual and additive effects, but still higher than the individual gene effects (Mathur & Horst ,1992). Egg mass is increased by 48 % in the combination of the *Na* and *F* genes (*Nana Ff*) compared with the normally feathered genotype (*nana ff*) under constant high temperatures (Haaren-Kiso *et al.*, 1994). It seems that introducing major genes such as *Na* or *F* into high producing lines or only into the sire or the female

parent line of the commercial product would be a quicker way to introduce heat tolerance and thus maintain or lose little of the most valuable performance traits. Males with such characteristics could also be used to upgrade indigenous chickens. Both the *Na* and *F* genes could be back-crossed into sire lines at the same time.

Gowe & Fairfull (1995) stated that whether the *dw* gene will be useful in parent stocks for the tropics, beyond its characteristics of reduced body size and bird space requirements and improved feed efficiency, depends on the economics of production of the region. Mathur & Horst (1989) advocated that the introduction of the *dw* gene should be attempted with medium sized or still heavier populations in order to utilise its favourable side effects on metabolism, feed conversion, persistency, mortality rate, and shell structure. The dwarf gene will perhaps be more useful in combination with the naked neck gene, the frizzle gene or both since the *Na* tends to increase the disadvantageous size of the egg of dwarf layers, and the *dw* gene improves feed efficiency (Mathur & Horst, 1992). In the study of Haaren-Kiso and colleagues (1994), the dwarf naked neck and the dwarf naked neck frizzle types (*Nana ff dw-*; *Nana Ff dw-*) showed best performance for all biological and economical efficiency traits under high temperature conditions.

1.3 The scope of the study

The majority of the studies aiming at developing heat-tolerant strains reported in literature were performed in controlled chambers, which were maintained at a constant pre-determined temperature. In addition, high temperature was generally associated with low humidity. Tests in controlled environments give valuable information about the productive physiological reaction of birds to environmental heat stress. However, they cannot completely represent the natural conditions, partly because the stressful effects of heat are compensated to a distinct degree by diurnal and seasonal variations. The responses of various genotypes in controlled environments and natural conditions are different showing distinct genotype x environment interactions, especially for egg production traits (Mathur & Horst, 1989). As a result, it is not clear whether selection

should be made under controlled high temperature conditions or under the variable ambient temperatures of a tropical climate. There is also no evidence that strains selected for different performance traits as well as heat tolerance in a constant temperature chamber do better under the variable conditions found in most tropical environments than the strains that were selected under variable temperate conditions (Gowe & Fairfull, 1995). Mathur & Horst (1994) and Leenstra & Cahaner (1991) suggested that it would be best to select under the prevailing climatic conditions where the birds are to be used.

In view of the concepts earlier described for both rural and urban poultry production development, a breeding strategy adapted for the specific conditions of the southern coastal region of Mozambique and incorporating the three major genes should be considered. Given the non-additive action of the genes described above and the variability of response in each environment, research is needed to clarify which combination of the selected genes is most efficient under the environmental and economic conditions of this specific location. In addition, as feed for poultry production available in Maputo is frequently of sub-optimal or variable quality, with crude protein the most affected nutrient, nutritional limitations should thus be considered on performance tests of the birds.

The hypothesis was that the selected genes are not equally responsive to the environment.

The hypothesis was challenged by testing whether the major genes for feather reduction (naked neck), feather curling and reduction (frizzle) and body reduction (dwarf) significantly contribute to the biological and economic efficiencies of a dual purpose layer strain under the climatic conditions of Maputo and a standard and a substandard nutrient regime.

The results should provide recommendations for future breeding policy and for the commercial exploitation of genotypes more suitable for peri-urban and rural poultry development programmes in the south coastal region of Mozambique.

2 LITERATURE REVIEW

2.1 Growth of pullets

In recent past, breeding companies stressed the importance of achieving a target body weight for a «ready-to-lay» pullet, with the usual main goal being to achieve these target weights with a minimum of nutritional input. Body weight at the end of rearing served as a convenient tool for evaluating the rearing period under practical conditions (Kwakkel, 1994) and might be an important feature for subsequent laying performance (Robinson & Robinson, 1991; Keshavarz, 1998). However, research on feeding strategies for layer pullets has become more focused on the growth pattern during development, rather than on target weights. Undoubtedly, a minimum body weight is necessary for the onset of lay, but the growth rate or the shape of the pullets' growth curve may give additional information on the performance ability than does pre-lay body weight *per se* (Kwakkel *et al.*, 1991). As commercial birds are maturing at earlier ages than previously, the key to successful rearing programmes might be the attainment of desired weight for age.

Growth is a complex biological process influenced by genetic and environmental factors, which is usually measured as change of body mass and composition of the individual over time. Growth can be expressed in absolute or relative terms. Absolute growth is the change in size per unit of time, the most common being age. The rate of growth is hence of great importance, since growth is a mutiplicative rather than an accretionary process. Absolute growth, however, relates growth to size and not to developmental maturity. Morphogenetic changes take place by relative growth as certain components of the living system increase at a higher or lower rate than others. Relative growth rate is represented by the ratio of weight gain during a given unit of time to average weight of the organism during the time period.

2.1.1 Multiphasic growth theory

The body weight curve is determined by the rates of deposition of chemical body components such as dry matter, crude protein, crude fat and ash, which are related to the bird's age. From a biological point of view, the deposition of these body

components in individual organs determines the physiological age and state of maturity of the pullet. Normally, if the nutrient supply is not limiting, each body component exhibits its own distinctive pattern of growth and functional maturation (Ricklefs, 1975). Consequently, there will be a variation in the nutritional demand of specific tissues and organs in the course of time, due to the biological forces in the development of these body constituents (Ricklefs, 1985).

Growth can be considered biologically as being a discontinuous process. The Cambridge school (Hammond, 1932 cited by Kwakkel, 1994) suggested by their classic growth order theory that growth is the result of sequential growth waves, each of which represents distinguishable stages of development of individual, functional body parts. More recently, it was demonstrated that growth could be described in terms of distinguishable growth phases or spurts by a multiphasic growth model (Koops, 1986). Component growth has a multiphasic nature. Each growth cycle might consist of growth spurts of specific body structures. Body weight gain in pullets can be described by a triphasic function (Grossman & Koops, 1988), but Kwakkel *et al.* (1993) found the most accurate fit by a tetraphasic growth model. According to the latter authors, growth in the first two phases seems to be related to the development of bones, muscles, and essential metabolic organs, and represents 82 % of mature body weight. Around 19 wk of age, a third phase or the pubertal growth spurt represents mainly growth of the reproductive tract and to a lesser extent of abdominal fat, representing an additional 10 % of the mature body weight. A strict interval of 14 to 15 days was observed between the peak of the pubertal growth spurt and onset of lay. The fourth phase at about 24 wk of age consists essentially of abdominal fat deposition.

2.1.2 Hormones and growth

Investigations on the role of hormones in avian growth have concentrated primarily on the effects of two substances, growth hormone (GH) and thyroid hormone. The first has been isolated from pituitary tissue while the second is synthesised by the thyroid glands.

High plasma concentrations of GH are observed during the period of rapid post-hatching growth whereas low concentrations are seen in older and adult chickens. Growth hormone is segregated in pulses approximately once an hour, in a pattern described as circhoral. The effect of GH on carbohydrate and lipid metabolism may be characterised as (1) increasing the free fatty acids in the circulation, which are then available as an energy source, and (2) decreasing lipogenesis and reducing glucose utilisation (Scanes, 1986).

Thyroxine (T_4) and triiodothyronine (T_3) have been shown chromatographically to be in thyroid tissue in chickens. There is evidence that T_3 is formed by extrathyroidal conversion of T_4 to T_3. The thyroid is necessary for normal growth and disruption of thyroid activity by surgical thyroidectomy results in growth retardation, feather structure alteration, and reduced gonadal function (Wentworth & Ringer, 1986).

2.2 Sexual maturity

Except in cases of severe feed restriction or physical abnormality, sexual maturity in the laying hen is inevitable. Commercial egg-laying hens, when given a conventional lighting programme (eg., a constant 8 h photoperiod to 17 weeks) and fed *ad libitum*, reach sexual maturity between 20 and 22 weeks of age. In the last two decades, mean age at 50 % rate of lay decreased by approximately 0.5 d per year. The continuing drive to maximise egg numbers as well as the current decrease in importance of egg size allows direct pressure to be exerted upon genetic selection for earlier age at first egg (Lewis & Perry, 1996).

2.2.1 Physiological pathways to sexual maturity

The system of reaching puberty is very complicated, and it seems therefore unlikely that only one factor is involved. The elucidation of the controlling factor(s) and the physiological pathways of sexual maturity has been a difficult task, because in many studies cause and effect were not always clearly distinguished. Timing of the onset of

lay may be determined by a number of interrelated factors, such as age and body weight as threshold factors (Dunnington *et al.*, 1983), body fat (Brody *et al.*, 1984), and lean tissue (Zelenka *et al.*, 1986). Several works stressed the importance of body composition over body weight as the primary determinant for onset of lay (Summers *et al.* 1987; Dunn & Sharp, 1990). The fat hypothesis has been rejected by Kwakell *et al.* (1995) on the grounds that, at the time of initial sexual development, energy is channelled towards fat deposition, a process that is governed by circulating estrogens, produced by the yet to be developed ovary. These authors demonstrated that a particular proportion of fat and fat-free tissue might be required before sexual organ development starts. Lewis *et al.* (1998) found that changes in plasma follicle stimulating hormone (FSH) concentrations are better correlated with changes in age at first egg than plasma luteinising hormone (LH) changes. Yet, the primary factor (or factors) that alters the sensitivity of the hypothalamic-adenohypophyseal-ovarian axis and initiates the setting of the endocrine feedback mechanisms inducing the release of the brain and gonadal sex hormones is still unknown (Kwakell *et al.*, 1995).

2.2.2 Interacting influences of light and nutrition

Age at sexual maturity is due, in part, to the genetic constitution of birds but it is also the result of the influence of many environmental factors. Light and nutrition exert very strong modifying influences upon the timing of maturity.

Sexual maturity can be delayed by either the qualitative and quantitative restriction of nutrient intake. Qualitative restriction has been achieved by the *ad libitum* use of high fibre or low lysine diets (Lee *et al.*, 1971). The degree of retardation of sexual maturity directly depends on the level of food restriction, both in quantity and duration. Regression equations produced by Lewis & Perry (1996) based on their own results and on trials from different researchers give account of a reduction of approximately 0.3 d per 1 % of feed restriction.

Body weight gain is a key factor in the determination of the timing of sexual maturity. An extreme example of the effect of body weight gain suppression was described by

Dunn & Sharp (1992) in dwarf broiler breeder pullets. The birds, which were either maintained on an 8 h photoperiod or given an increase in photoperiod to 20 h at 22 wk of age, had their body weight restricted to 1 kg until 24, 36 or 52 wk by rigid control of food intake. No groups started egg laying until their daily allocation of food was increased to 120 g, irrespective of light treatment.

Pre-pubertal changes in photoperiod whether naturally gradual and continuous, progressively increasing or decreasing, or abrupt and singular exert very strong influences upon the timing of sexual maturity. Morris (1967) stated that photoperiodic responses are more influenced by changes in daylength than by the duration of light at any given moment in time, which was later confirmed by Lewis *et al.* (1996). Photoperiod manipulation can be used to advance or delay age at sexual maturity by anticipating or postponing the age at which pullets are exposed to an increased photoperiod. However, photoperiodism is far from absolute as the bird undergoes ovarian development regardless of photoperiodic duration, and becomes sexually mature at about 5 months of age under a wide variety of lighting regimes. On the other hand, the sexual response of the immature hen to an increase in photoperiod is not the same at all ages. Robinson et al. (1996) found that the time required reaching sexual maturity from the age of photostimulation decreases as the latter increases.

Under natural lighting conditions the variation in age at sexual maturity will depend on the latitude, and the time of year of the hatching. In both Northern and Southern hemispheres, winter-hatched pullets have the most advanced and summer-hatched pullets the most retarded maturity.

2.3 Stress physiology in poultry

Stress denotes the magnitude of forces external to the bodily system that causes a strain, i.e., a displacement from its resting state. The acclimatisation of an animal to the surrounding environment occurs through physiological adjustments or changes within its lifetime that reduce the internal displacement from the resting state caused by

stressful changes in the natural climate (Yousef, 1985). The capacity of the fowl to survive high temperature depends on a number of factors including duration of exposure, the rate of temperature change, the maximum temperature and the diurnal variations before and during the exposure. Poultry adapt to hot environments following previous exposure to high temperatures, increasing the upper and lower temperatures that define their thermoneutral zone and lethal temperature (Whittow, 1986), and increasing the temperature at which panting begins. The length of time that heat tolerance will persist following high temperature exposure is not well defined (Ernst, 1995).

2.3.1 Heat stress and the maintenance of body temperature

Birds are «homeotherms», which means that they maintain a relatively constant deep body temperature. Birds are also «endotherms», a term indicating that they are able to increase their body temperature by generating a considerable amount of heat within their tissues instead of relying on heat generating directly from their surroundings. In general, the features of thermoregulation are similar in birds and mammals. However, there are some differences between the two groups that have a direct influence on the manner in which they regulate body temperature. The plumage of birds has the dual function of flight and the provision of thermal insulation. Feathers are a good insulation material, which is advantageous at low temperatures, but hinder the dissipation of heat from the skin at high temperatures. The absence of sweat glands in birds places the onus of evaporative cooling on their respiratory mechanisms (Whittow, 1986).

The environment influences an animal through the exchange of energy. The net energy stored in the tissues equals the difference between energy intake and energy loss. Metabolism of food and high environmental temperature are potential sources of energy while low environmental temperature and the maintenance of normal body temperature are potential expenditures of energy (Etches *et al.*, 1995). Homeothermy is maintained as a result of a sensitive balance between heat production and heat loss. In chickens, body temperature is maintained within a relatively narrow range that is usually reflected by the limits of a circadian rhythm in deep (or core) body temperature. The upper limit

is about 41.5 °C and the lower limit is approximately 40.5 °C. The zone of thermoneutrality is where basal heat production is minimal and body temperature is maintained within the normal range. It lies between the lower and the upper critical points, which are, respectively, the environmental temperatures of 18 and 26 °C. At temperatures above the thermal maximum, core body temperature starts to rise, with a resulting increase in metabolic rate. If body temperature is increased until it exceeds 42 to 43 °C, there will be a damage to the central nervous system and other structures (heat stroke), with fatal consequences (Bligh, 1985). The upper lethal temperature is the maximum environmental temperature above which death occurs.

2.3.2 Heat loss mechanisms

Heat dissipation and maintenance of homeostasis involve the functional integration of several organs. During exposure to high ambient temperatures, chickens maintain a near-constant body temperature by controlling evaporative or insensible heat loss through panting (i.e., increase in respiratory ventilation) and nonevaporative or sensible heat loss (i.e., radiation and convection) (Marder & Arad, 1989; Yahav *et al.*, 1998).

Respiratory evaporation is a very important source of heat dissipation. Panting is first detectable at the upper limit of the thermoneutral zone. This specialised form of respiration dissipates heat by evaporative cooling at the surfaces of the mouth and respiratory passageways. The advantage of such thermal polypnoea on the bird's thermoregulation, however, is attended by a higher gas-exchange rate in the lung and an increased pulmonary elimination of carbon dioxide from the blood with some worsening effects on blood-gas composition, acid-base balance and electrolyte status (Pech-Waffenschmidt, 1992). Therefore, the physiological mechanisms that are invoked by birds exposed to high temperatures must meet the opposing demands of thermoregulation and respiratory alkalosis. It is believed that, at an ambient temperature of 32 °C and relative humidity of 50-60 %, hens reach the maximal ability to lose heat through evaporation (Wilson, 1948 cited by Etches *et al.*, 1995).

Other heat-loss mechanisms, though being less effective than panting, have been considered to improve the bird's thermoregulation. Heat is dispersed through anatomical characteristics in birds that provide increased blood flow to surfaces that can effectively transfer heat by radiation and convection. The vascular system in the legs and feet of fowl contains arteriovenous heat exchange mechanisms that facilitate the dispersal of heat through these insulated surfaces. Convection is mainly affected by peripheral blood flow, body surface, and body covering. The increased blood flow to the body periphery during heat stress is reflected in elevated skin temperature and hence the unfeathered parts of the bird are more involved in the sensible heat emission than the covered ones (Richards, 1976). A natural plumage reduction, achieved by the introduction of the naked-neck (*Na*) and the frizzle (*F*) gene, led to higher body temperature, improved heat loss and lower core body temperatures (Pech-Waffenschmidt *et al.*, 1995).

2.3.3 Consumption of feed and water

Water consumption increases when chickens are exposed to high ambient temperatures, and survival in a hot environment is dependent upon the consumption of large volumes of water (Etches *et al.*, 1995). Voluntary feed intake is reduced in response to high environmental temperatures, to minimise endogenous heat production and avoid a lethal increase in body temperature (Yahav *et al.*, 1996). Fasting prior to heat stress increases survival time, and the time required to reach a lethal body temperature is inversely proportional to the fasting time. Therefore, although decreasing food intake only during the period of acute increases in temperature does not affect mortality, decreases in food intake associated with increases in environmental temperature may well reflect a survival response (McCormick *et al.*, 1979). The increase in water consumption occurs immediately, whereas the decrease in feed consumption is delayed until several hours after exposure to higher temperatures (May & Lott, 1992). The immediate increase in water consumption meets the immediate requirements of evaporative cooling from respiratory surfaces and the associated decline in food intake reduces the contribution of metabolic heat to the total heat load that requires dispersion.

Different physiological mechanisms that control fed intake have been hypothesised, but the thermostatic and the chemostatic theories seem to explain most of the observed factors related to voluntary feed intake of hens. According to the first theory, heat produced by heat increment of the diet raises the temperature of the body and the hypothalamus responds by adjusting total quantity of food consumed (Smith, 1973). The chemostatic mechanism involves the concentration of certain chemical compounds in regulatory organs and explains the observed inverse relationship between dietary energy level and feed intake (Ahmad *et al.*, 1974).

2.3.4 Temperature and humidity interaction

In the tropics, natural environments are characterised by daily and seasonal fluctuations in the two main environmental factors, temperature and humidity. Daily cycling variation allows to a certain extent for an alleviation of the stressful effects of high temperatures through nocturnal dissipation of the heat stored during the hottest part of the day. In most latitudes, seasons are characterised by extreme and reversed climatic variation, making birds that perform well in the one environment to show reduced or even impaired productivity in the other.

Heat strain is most commonly considered to be a product of ambient temperature and relative humidity. High humidity reduces evaporative loss from the skin and respiratory membranes of poultry and thereby increases the negative effects of high temperature. Yahav *et al.* (1995) have demonstrated that the interaction between the two environmental factors in birds is complex. At 35 °C, chickens exposed chronically to 60-65 % RH were able to control rectal temperature around normothermic values known for the domestic fowl, whereas both hyperthermia and respiratory alkalosis developed at higher (70-75 %) or lower (40-55 %) relative humidity. Energy maintenance needs were lowest at 60-65 % RH and the authors suggested that this result from less energy being invested in thermoregulation.

Temperature and humidity can be expressed as an index of stress. According to Yousef (1985), the temperature-humidity stress index (THI) is the most practical means for

measurements of the thermal environments and for assessing the exposure of animals to heat stress in a given area.

2.4 Productive penalties of heat stress

Thermal environments are a constraint on the performance of chickens in intensive or extensive production systems. The penalties to efficient performance (production, reproduction, feed conversion, health) and wellbeing of the animals can be severe. However, these are dependent on many factors, such as the animal's normal level of production, age, prior conditioning, and the degree to which the nocturnal environment provides release of the stored heat. If physiological and behavioural processes are inadequate to cope with a hot environment, the animal decreases the daily feed intake to reduce metabolic heat production, as earlier explained, with a resulting decline in the productive function (growth rate, egg laying). In general, high-producing birds have higher feed intakes per unit of body weight, which result in greater metabolic heat and, therefore, increased heat stress. The reduction in appetite has been estimated to be 1.5 % for each one degree rise between 21 °C and 30 °C and about 4.6 % per degree rise between 32 °C and 38 °C (Payne, 1966).

Under intensive management both the direct and indirect effects of high environmental temperature can change not only the number of eggs produced by a hen in a given period but also the quality of these eggs. The poor performance of laying hens kept at high temperatures has been attributed to reduced food intake (Austic, 1985). However, only some of the limitations imposed on the performance and body weight of laying hens by hot environments are related to food intake. The pair-feeding experiment conducted by Smith & Oliver (1972a) showed that only 40 to 50 % of the effects of heat stress on egg weight and rate of lay could be attributed to reduced food intake, while egg quality was mainly affected by heat *per se* (non-food-mediated). In a different work, Smith & Oliver (1972b) found that, under high protein diets egg production was not adversely affected by temperatures as high as 32 °C, although hens experienced a considerable initial loss in body weight. They also found that the effect of high

temperature on body weight is progressive and increases both with time and the degree of temperature increase. David *et al.* (1972) have shown that, in hot environments egg production can be maintained at high levels at the expense of a considerable amount of body weight being metabolised.

Temperature during growth might significantly influence the response of hens to high temperatures during lay. In natural (Njoya & Picard, 1994) or controlled (Kyarisima & Balnave, 1996) conditions, performance of pullets in a hot environment was improved by rearing them in a cool environment, the response being related to an increased food intake. However, it appears that rearing the pullets in a hot dry or humid environment does not seem to acclimatise them to similar climates encountered during the laying period (Njoya & Picard, 1994).

Elevated temperatures can also disrupt normal endocrine functions resulting in reduced reproductive capabilities and altered health status, which are also penalties to performance (Hahn, 1985).

2.5 The efficiency of feed utilisation in hot environments

Among the many factors that determine net income for the commercial egg producer, feed efficiency has taken on increased significance in recent years. In particular, nutrition x environment interactions are of interest in modern poultry. Temperature is particularly important because it influences nutrient requirements and the digestibility of dietary nutrients. However, voluntary feed intake is governed by factors other than temperature, which can obviously affect the amount of food consumed under hot environments. The onset of lay and variations in the rate of egg production complicate the interactions between nutrient requirements and environmental temperature. Furthermore, such interactions are buffered in the short term by changes in body tissue reserves, as the hen can, within limits, mobilise body reserves to compensate for deficiencies in nutrient intake (Scott & Balnave, 1991).

Dietary adjustments are often made to overcome the reduced performance due to hot weather conditions. Studies with growing pullets and laying hens are in agreement that increased aminoacid, energy or calcium levels or dietary self-selection cannot effectively compensate for the reduced feed intake frequently observed at the higher environmental temperatures (Blake *et al.*, 1984; Smith & Teeter, 1993). Moreover, paired-feeding studies show that reduced traits were not simply the result of a reduction in nutrient intake but also the direct effect of heat stress on the hen (Emery *et al.*, 1984). Mahmoud *et al.* (1996) demonstrated that in heat stressed females the typical pattern of estradiol was depressed and the calcium uptake by duodenal cells was lower and postulated that this might be a critical factor in the detrimental effects of heat stress on egg numbers, eggshell characteristics and skeletal integrity.

An examination of the variables commonly used in partition equations to predict metabolizable energy intake shows that the rates of egg energy deposition and body energy change are almost constant between 10 and 25 °C. Above 25 °C, energy intake falls much more quickly than heat loss, the difference being accounted for the reductions in egg and body energy. Because egg output remains constant over a wide range of temperatures while energy intake is falling, it follows that the gross energetic efficiency of egg production improves with increasing temperature (Marsden & Morris, 1987).

Research workers have approached the problem of determining the protein requirement of layer hens from the standpoint of grams of protein intake per hen per day. The earlier works of Lillie & Denton (1967) and Thayer *et al.* (1974) showed that a minimum of 14 g/hen/day was adequate for egg production, but that a slightly higher amount, 15-16 g/hen/day was necessary for the maintenance of egg weight or body weight. Reid & Weber (1973) found significant improvements in egg production with increased protein consumption over 13 g/d at 21 °C, but no increase in production at 35 °C. By multiple regression analysis, they concluded that energy intake was the limiting factor for egg production at the latter temperature, though stating that a number of other factors might adversely affect egg production at higher temperatures. It appears that small increments in protein supply, close to the optimum, result in equal proportional responses in rate of

lay and in egg size. When protein supply is below the optimum to the extent that output is below 90 % of the potential of the flock, the expected reduction in rate of lay is greater than the expected reduction in egg size (Morris & Gous, 1988).

Feed is used for maintenance and for production. In *ad libitum* fed laying hens, feed energy for maintenance represents about 44 % of gross energy consumption, being related to metabolic body weight. Production energy requirements, which are about 25 % of gross energy intake are related to egg mass production and, when relevant, to body weight gain (Van Es, 1989).

A considerable and steady improvement in feed efficiency was achieved in recent past. Because maintenance requirements account for the major proportion of feed consumption, body weight reduction will be very significant for feed efficiency improvement. However, the possibilities of utilizing this strategy in a continuous selection programme are limited, since body weight is closely related to egg weight. Body weight below a certain threshold (1.5 kg) impose a serious depression in egg mass (Luiting, 1990). Under conditions of high temperature and humidity, loss of appetite resulting from too much reduction in body weight cause difficulties with regard to the support of high egg mass. An alternative approach to body weight reduction is provided by the sex-linked dwarfing gene. Feed efficiency is improved by about 25 % in broiler breeder females and 13 % in medium-size laying stocks (Mérat, 1990).

2.6 Major genes for improved tolerance to heat stress

Particular genes are known to improve heat endurance through different pathways, such as:

- increase in heat loss by means of greater convection, conduction and radiation;
- decrease in metabolic heat increment due to lower basic metabolism;
- increase of the upper limit of critical body temperature.

The naked neck (*Na*) and the frizzle (*F*) are genes that diminish the insulating power of the bird's plumage and thus are associated with increased heat loss. The reduction in feathering intensity is directly associated with increase in body surface temperature. At 34 °C, the surface temperature of naked neck and frizzle birds was recorded as being 5 °C higher than that of a normal feathered bird. This not only helps the adaptation process through increased sensible heat loss but also relieves panting, leading to fewer disturbances in the acid basic balance (Horst & Mathur, 1994). The *Na* gene has proven to thermoregulate at low temperatures and to be effective in heat dissipation in constant heat stress, yet showed no superiority under diurnal cyclic conditions (Yahav *et al.*, 1998). In egg-type birds tested at higher temperatures, the gene improved heat tolerance as indicated by higher egg production, better feed efficiency, earlier sexual maturity, larger eggs with possibly fewer cracks, and lower mortality when compared with normal feathered birds with similar genetic background (Mérat, 1990). The studies of Haaren-Kiso *et al.* (1988, 1992) have shown that the frizzle gene (*F*) increases egg numbers and favourably affects egg weight, feed efficiency and viability under high temperatures.

The main effect of the dwarf gene (*dw*) is to reduce the body weight of the hemizygous birds. Some reports show an advantage of the small-body-weight dwarf over comparable normal hens, as measured by less depression in egg number and egg weight at high temperatures. Other reports, however, show no relative advantage in hot conditions (Mérat, 1990). Nevertheless, there is a body of evidence to show that body size strongly influences the bird's capacity to acclimatise and to survive heat stress, as a small body size lowers internal heat production and allows faster heat dissipation (Gowe & Fairfull, 1995).

The single and combined effects of the three major genes mentioned were widely investigated in a medium heavy layer strain (Horst, 1998). The results underlined the advantage of these genes, especially the dwarf, when egg number was expressed on a metabolic body weight basis. They also showed significant interactions between the major genes as well as between the genes and the environment, emphasising the need for testing the adaptability of the gene combinations at each specific location.

3 MATERIALS & METHODS

3.1 Experimental birds and management

Day-old chicks were obtained from the Institute for Animal Basic Sciences of the Humboldt University of Berlin and transported to Maputo, Mozambique (25°58′S, 32°35′E) in January and August 1996. The pullets were the offspring of a Dahlem Red commercial male line heterozygous for the naked neck (*Na*), frizzle (*F*) and dwarf (*dw*) genes and a Rhode Island White female line homozygous for the normal alleles of the three genes. The gene for light downs (*Li*) was incorporated to allow colour sexing of day-old chicks. Eight different hybrid combinations of genes for body size and feather coverage, constituting eight different genetic groups or genotypes were segregated randomly from such a mating plan as follows:

Phenotypic classification	Genetic specification	No. of birds studied
Normal feathered normal size	*nana ff Dw- li*	94
Naked neck normal size	*Nana ff Dw- li*	63
Frizzle normal size	*nana Ff Dw- li*	93
Naked neck frizzle normal size	*Nana Ff Dw- li*	65
Normal feathered dwarf	*nana ff dw- li*	102
Naked neck dwarf	*Nana ff dw- li*	78
Frizzle dwarf	*nana Ff dw- li*	123
Naked neck frizzle dwarf	*Nana Ff dw- li*	79

The pullets were conventionally raised on floor and fed *ad libitum* egg type pullet commercial diets in a two-phase system, from 0-6 wk and 7-18 wk (Table 3.1). All chicks were exposed to continuous lighting for the initial 72 h and then to the prevailing natural daylight. The sexes were reared separately. At three weeks of age, frizzle and normal feathered birds were separated. Dwarf and normal size pullets were divided at 10 weeks of age, and reconfirmed at 15 wk based on measurement of the shank. Birds were vaccinated in accordance with the recommendations of the local veterinary authority. At

18 weeks of age the pullets were moved to individual cages in a laying house with low cement block walls extended to the roof with wire netting.

3.2 Experimental design

Birds were fed *ad libitum* two laying diets based on corn, wheat bran and soya meal with different protein content and ME:protein ratios and similar amino acid content, as indicated in Table 3.1. For the purpose of this work, laying diet 1 was considered having a high protein content and laying diet 2 a low protein content, being referred hereafter as HP and LP, respectively.

Table 3.1
Nutrient composition of diets

Period	Growing		Laying	
	0-6 wk	7-18 wk	18-96 wk	
	1st phase	2nd phase	Diet 1	Diet 2
Measured				
CP, %	19.50	15.00	16.20	14.40
Calcium, %	0.80	1.00	3.60	3.62
P, %	0.40	0.50	0.64	0.66
Calculated				
ME, kcal/kg	2,900	3,060	2,650	2,670
ME:P ratio	148	204	164	185
Lysine, %	0.90	0.64	0.80	0.80
Methionine, %	0.36	0.29	0.35	0.35

Seasonal environmental effects of climate and photoperiod were studied during the growing and laying periods in two experiments. The experiments were designed to elapse in opposite climatic and photoperiodic conditions and are, for the purpose of this study, considered as levels of the experimental factor named Season. The duration and the main environmental characteristics of each period and experiment are summarised in Table 3.2. The terms summer and winter are used also throughout, identifying the

prevailing climate at the beginning of the phase (growing or laying) to which they are referred.

Table 3.2
Schedule and main environmental characteristics of the periods studied

Phase (duration)	Exp.	Month/Year	Photo-period	Prevailing climates
Growing	1	Feb 96 – Jun 96	D [1]	H-MH [2]
(18 wk)	2	Aug 96 – Dec 96	I	MH-H
Laying,				
1st cycle	1	Jun 96 – Jun 97	I-D	MH-H-MH
(52 wk)	2	Dec 96 – Dec 97	D-I	H-MH-H
2nd cycle	1	Jun 97 – Nov 97	I	MH-H
(24 wk)	2	Dec 97 – May 98	D	H-MH

[1] D = Decreasing; I = Increasing
[2] MH = Mild hot; HH = Hot

The experimental design was, therefore, eight genotypes distributed equally to treatments where treatments were distributed to rows randomly. The individual females of each genotype were distributed randomly to individual cages within dietary treatment.

3.3 Data collection and experimental procedures

Ambient temperature (Ta) and relative humidity (RH) were recorded inside the poultry buildings three times a day. Individual live weights of birds were measured on arrival in Maputo (0 wk) and fortnightly up to week 18. During the laying cycle, birds were weighed every 4 weeks. The age at first egg was used to determine the sexual maturity (SM). Age, body weight and egg weight at the onset of laying were individually recorded. Double-yolked eggs were discarded from the calculation of the initial egg weight. Egg production, including abnormal (soft-shelled, double-yolked and yolkless) eggs was recorded daily and all eggs laid on three consecutive days each week were weighed automatically to the nearest 0.01 g. Feed consumption was measured every

week by a weigh-back of residues in the individual feed troughs without correction for wastage.

Egg quality of 12 randomly selected hens within treatment (N=384) was measured at 28, 40 and 64 weeks of age of the pullets. After collection, eggs were immediately weighed and stored at 20 °C for quality evaluation in the following day. Breaking strength was measured with an appropriate device (Wazau) by applying a gradually increasing vertical force along the long axis of the egg. Eggs were broken out, albumen height measured manually in a device specially prepared and components carefully separated. Shells were weighed fresh with membranes and allowed to dry at room temperature. Shell thickness excluding membranes, was measured with a micrometer at two locations in the equatorial area.

3.4 Calculated traits

Temperature-humidity index (THI)

Selected production traits have been related to the Temperature-Humidity Index (THI), which is a derived statistic computed from the relation calculated by Bosen (1959):

$$THI = t_{db} + 0.36\, t_{dp} + 41.2$$

where t_{db} = dry-bulb temperature in °C (maximum temperature at 14:00), t_{dp} = dew-point temperature in °C. The dew-point temperature is the temperature where condensation first occurs when air-water vapour mixture is cooled at constant pressure and was calculated as follows: t_{dp} = dry-bulb temperature at 14:00 minus wet-bulb temperature at 14:00. The resulting value was used in the hygrometric tables (Instituto Nacional de Metereologia, Mozambique) to arrive at the corresponding dew-point temperature for the atmospheric pressure of Maputo. Safety categories were based on The Livestock Weather Safety Index advisory categories (Anonymous, 1970).

Growth and performance

- Relative growth rate was calculated as $(dW/dt)/W$ where W is the body weight and t the time in weeks (Hancock *et al.*, 1995).
- Chronological age and body weight of the pullets were standardised by means of the percentage proportion to the onset age and body weight (Zelenka *et al.*, 1986).
- Proportion of onset body weight was calculated by dividing the body weight of each female at selected ages by the body weight at first egg.
- Performance traits were calculated by surviving hen in each period.
- Mortality was considered separately and its effects on performance evaluated economically.
- Persistence was calculated for the first laying cycle as the time at which 60 % of the total production of each individual was attained, and as the ratio between the number of eggs produced in the third (31-52 wk) and the second (9-30 wk) laying periods.
- Egg mass was calculated by multiplying the total number of eggs produced in a week by the average egg weight of that particular week, without correcting for abnormal eggs.
- Feed intake was divided by the mean metabolic body weight in each period to give the ratio $FI/BW^{0.75}$.
- Feed efficiency is the amount of feed consumed per unit of egg mass.
- Feed conversion is the feed required per dozen eggs.
- Biological efficiency is the ratio between daily egg mass and the mean metabolic body weight.
- Productivity was calculated as the total number of eggs produced per mean metabolic body weight.

Equation used for the increase in egg weight with hen age

The equation used in this study relating egg weight (Y) with age (t) is of the form:

$$Y = A - Br^t$$

where A represents the mature egg weight, B represents the range in egg weight from t=0 (start of lay) to the asymptote mature weight, while r indicates the rate at which the mature weight is approached ($r < 1$) (Weatherup & Foster, 1980).

Economical evaluation

Eggs were graded and valued according to the following weight classification and prices:

Size class	Egg weight	Price MT [1]/dz egg
Peweee and small	under 47.3 g	10,000.00
Medium	47.3 – 54.2 g	13,000.00
Large	54.3 – 61.4 g	13,000.00
Extra-large and Jumbo	61.5 and over	15,000.00

[1] MT = Metical (Mozambican currency; 2,200 MT:1 Rand)

The following price structure was used in the remaining calculations: 13,000 MT per dozen eggs not graded; 4,600 MT per kg of feed; 75,000 MT per point-of-lay normal size pullet and 65,000 MT per point-of-lay dwarf pullet. The salvage or residual value of a spent hen at the end of the first cycle was considered as being 40 % of the bird's initial price.

The various indicators used were calculated as follows:

$$\text{Contribution margin} = 100 - \left(\frac{\text{Feed cost} + \text{Net cost of pullet}}{\text{Income eggs}} * 100 \right)$$

$$\text{Break - even output} = \frac{\text{Cost of replacement pullet}}{(\text{Selling price/egg}) - (\text{Feed cost/egg})}$$

$$\text{Break - even feed price} = \frac{\text{Income eggs - Net cost of pullet}}{\text{Feed consumed}}$$

$$\text{Break - even selling price/dz egg} = \frac{\text{Feed cost + Net cost of pullet}}{\text{No. of eggs sold}}$$

3.5 Statistical analysis

Dietary (where applicable), seasonal and genetic effects on the different observed and calculated traits were analysed using individual values of birds by means of the General Linear Model (GLM) procedure, according to the following models:

$$Y_{ijklm} = \mu + D_i + S_j + Na_k + F_l + dw_m + I_{1\rightarrow n} + e_{ijklm} \quad (1)$$

$$Y_{ijklm} = \mu + D_i + S_j + G_k + I_{1\rightarrow n} + e_{ijkl} \quad (2)$$

where μ = overall mean, D = laying diet; S = Season (or Experiment); *Na* = naked neck locus; *F* = frizzle locus; *dw* = dwarf locus; G = genetic group (or genotype); I = interactions; e = error term.

Means for the genetic groups in Model 2 were compared by Dunnett's pairwise multiple comparison t-test against the normal size normal feathered group *nana ff Dw-*, set as control. For selected variables and whenever statistical similitude (P>0.05) between feathering types within size type would allow it, data was combined and presented by body size group. Egg quality was analysed according to the models described above using GLM Repeated Measures procedure with age set as the between subjects factor. Percentage traits were subjected to the angular transformation prior to analysis. All statistical analyses were performed with the SAS programme (SAS Institute, 1994).

4 RESULTS

4.1 Climatic and photoperiod variations

Room maximum and minimum temperatures and relative humidity during the overall period of study are plotted in Figures 4.1 and 4.2, and the values presented in Annex 1. Monthly average daylight length is illustrated in Fig. 4.3. The results show that the terminology used in Table 3.2 to characterise both the climate and the photoperiod within the experiments was appropriate. Additionally, they confirm that the design of the experiments allowed for each physiological and productive phase to be studied in opposite environmental conditions, thus guaranteeing an averaged year-round evaluation of the birds in this particular location.

Growing phase

During the growing phase of the pullets, the room average temperature diminished from 28.7 °C (February) to 20.1 °C (June) in Exp. 1 and increased from 20.7 °C (August) to 28.1 °C (December) in Exp. 2. Higher temperatures were thus prevailing in the first and the second half of Exp. 1 and Exp. 2, respectively. The average relative humidity showed lower variation throughout the growing phase, as it declined from 72 to 69 % in Exp. 1 and increased from 69 to 72 % in Exp. 2. The length of daylight diminished from 13.2 hr to 10.3 hr in the first experiment and increased from 11.1 hr to 13.5 hr in the second.

Laying phase

The first cycle (LC I, 52 weeks) of the laying phase comprised three different climatic environments. The first elapsed during the first 8 weeks after housing, and the second and the third had a 22-wk duration each. Table 4.1 summarises the climatic data for each sub-period. In Exp. 1, the first sub-period (1-8 wk) was characterised by mild hot weather, the second (9-30 wk) by a gradual increase to very hot, and the third (31-52 wk) by a decline to mild hot. In Exp. 2, the climatic conditions in each sub-period were reversed. Climate was very hot in the first sub-period, gradually declined to mild hot in the second, and was followed by an increase to hot in the third. Temperature differences between the first and the second experiment were -7.6 °C (1-8 wk), +4.8 °C (9-30 wk),

and -1.3 °C (31-52 wk). In the second laying cycle (LC II, 24 weeks), temperatures were rising from mild hot to hot in Exp. 1 and decreasing from very hot to mild hot in Exp. 2. During this period, the average temperature in the first experiment was 2.4 °C lower than in the second. Average relative humidity was fairly constant in all the periods considered. Maximum differences between experiments (3.9 %) were observed in the first sub-period of the first cycle.

In the first experiment, daylight length gradually increased from 10.40 to 13.40 hr during the first half of LC I and declined to 10.3 hr in the second. In Exp.2, photoperiod decreased from 13.4 to 10.3 hr in the first 26 weeks of laying and increased to 13.2 hr in the second half of the cycle. During the second cycle of production, photoperiodic conditions in each experiment were similar to those prevailing in the first half of the first productive year.

4.2 The path to sexual maturity

4.2.1 Growth to sexual maturity

Probability levels and least square means of main and interaction effects at selected ages are presented in Tables 4.2 to 4.4. Season of growing was a highly significant source of variation of body weight of pullets ($P<0.001$). At 8 weeks of age, body weight of those raised from August to December (winter pullets, Exp. 2) was 7 % heavier than the ones growing from February to June (summer pullets, Exp. 1). At the end of the rearing period, summer pullets weighed 4 % more than winter pullets.

Averaged over the experiments, the *Na* gene had no influence on body weight of pullets. However, the interaction with season at 8 weeks of age shows that naked neck pullets compared with their normal-necked siblings were 2 % lighter in Exp. 1 and 4 % heavier in Exp. 2 ($P<0.05$). Birds carrying the *F* gene weighed 2 % less than the fully feathered ones at the end of the growing phase ($P<0.05$). At 18 weeks of age, the reduction in body weight caused by the sex-linked dwarfing gene was, averaged over feathering types,

approximately 32 % ($P<0.001$). The occurrence of a season x *dw* interaction at this age reveals that the difference between body size groups was 5 % greater in the first than in the second experiment ($P<0.05$).

Table 4.5 shows the LS-means by genetic group. At both ages, none of the three feather-reduced non-dwarf groups was different from the normal feathered type, despite the lowest body weight of the frizzle birds. Among the dwarfs, the normal feathered group was heavier than the remaining three, both at 8 and 18 weeks of age. Fig. 4.4 depicts the body weight of pullets in each experiment. It is worth noting that the greatest difference between experiments at 18 weeks occurred in both naked neck and frizzle non-dwarf females, due mainly to their lower body weight in the second experiment.

Body weight development over time is illustrated in the growth curves of normal and dwarf females plotted in Fig. 4.5. Initial body weight was similar among groups in both experiments but different patterns of growth occurred thereafter. The depressing effect on body weight resulting from the higher environmental temperatures can be observed during the first two months of the rearing period in Exp. 1. Body weight was seen to increase linearly throughout the remaining weeks, as temperature diminished. The situation was reversed in Exp. 2, where high temperatures influenced growth after the 8th week of age, thus conferring a more linear trend to the respective curve as opposed to the sigmoid-shaped curve of Exp. 1.

Body weight at the end of the growing period permanently influenced body weight throughout the subsequent stages of production. This is illustrated in Fig. 4.6, where relative growth rate at each age was plotted against the corresponding body weight transformed to its natural logarithm. Potential mature body weight corresponds to the point where relative growth rate becomes zero and the potential rate of decay in growth, i.e. the rate at which the bird matures is given by the slope of the linear function. Averaged over body sizes, the asymptotic mature weight of the pullets in the second experiment was 25 % lower than that in the first, as a result of the depressing effect of higher temperatures applied during the late stages of growth.

Body weights within body size groups were expressed as a proportion of weight at sexual maturity, i.e. the maturity index, and are presented in Fig. 4.7. It is noticeable from the figure that Exp. 2 birds were maturing faster than their replicates in Exp. 1, since at each age body weight relative to the onset body weight, was higher. It is also noticeable that while the rate of sexual maturing was similar in both body size groups in the second experiment, dwarf pullets were maturing more slowly than their normal siblings in the first. This differentiation was made visible after the 10^{th} week of age, thus illustrating the above-mentioned interaction between the *dw* locus and the season of rearing.

As populations differed in age at sexual maturity within and between seasons, age was also described in terms of degree of maturing by expressing chronological age as percentage of age at sexual maturity and was plotted against observed body weight (Fig. 4.8). This standardisation placed both body size groups on the same physiological scale and shows that for equivalent body weight, pullets in the second experiment were sexually more developed than those in the first.

4.2.2 Sexual maturity

Probability levels and LS-means of main and interaction effects on traits at sexual maturity (age, body weight, and initial egg weight) are shown in Tables 4.6 to 4.8.

Age at first egg

Growing season significantly influenced sexual maturity of the pullets ($P<0.001$). Birds raised from February to June, when both photoperiod and temperature were decreasing, were on average 17 days older at onset of lay than those grown from August to December under increasing daylight length and temperature. Similar age at sexual maturity was observed in females carrying either the naked neck or the frizzle gene. However, naked neck birds in comparison with their normal-neck siblings matured 4 days later in the first experiment and 2 days earlier in the second, as revealed by the interaction between these two factors ($P<0.01$). Averaged over the two experiments, the dwarfing gene delayed sexual maturity by 4 days ($P<0.001$), which resulted from a 7-day

delay in the first experiment and similar onset in the second. Consequently, the difference in age at first egg between the first and the second growing seasons was 13 and 20 days among the normal and the dwarf birds, respectively.

Averaged over the two experiments, no significant differences on age at sexual maturity occurred between the seven genetic groups and the normal type (Table 4.9). However, it is worth noting that whereas similar ages were observed among the normal size birds, all the feather-reduced types matured later than their normal feathered siblings within the dwarfs.

Onset body weight

Body weight at sexual maturity was significantly influenced by season of growing ($P<0.001$), as pullets raised in the first experiment were 252 g heavier than those in the second. The *F* gene was associated with lower (2 %) onset weight ($P<0.05$) whereas dwarf pullets were 32 % lighter at the first oviposition than their normal size counterparts ($P<0.001$).

The proportion of the onset weight at juvenile (8-wk) and mature (38-wk) age is presented in Tables 4.10 to 4.12. Season of year determined differences in both proportions ($P<0.001$). At 8 weeks, winter pullets had already a higher proportion of the onset body weight than summer pullets, which was maintained at 38 weeks of age. Normal size and dwarf birds alike attained approximately one third of the onset body weight at the juvenile age, whereas a significantly lower proportion was observed among dwarf hens in comparison with their normal size counterparts at mature age ($P<0.001$). The latter difference resulted from the lowered proportion observed in the first experiment, as revealed by the season x *dw* interaction ($P<0.01$). Similarly, mature body weight relative to that at sexual maturity in naked neck birds was lower in the first experiment though similar in the second ($P<0.05$). Lower proportion of onset weight at mature age was observed in birds fed the diet with lower protein content ($P<0.001$), which resulted from lower body weight at 38 weeks of age.

At 8 weeks of age, the two naked neck non-dwarf groups showed a significantly higher ($P<0.05$) proportion of the body weight attained at sexual maturity than the control group, as indicated in Table 4.13. At mature age, however, proportions were similar. Reversibly, the dwarf females, which had similar proportion at juvenile age, showed lower values than the control at 38 weeks of age.

Initial egg weight

The first eggs laid by summer pullets weighed 5.5 g more than those laid by winter females ($P<0.001$). A season x *dw* interaction ($P<0.001$) shows that the difference in the initial weight of eggs produced by normal and dwarf pullets was lower in the first (1.3 g) than in the second experiment (4.5 g). An interaction between the *F* gene and the laying diet reveals that initial eggs of frizzle birds were smaller in the high protein diet (+0.9 g). Table 4.14 presents phenotypic correlation between initial egg weight and other traits at sexual maturity by body size group and experiment. The coefficients show that, in both experiments, the weight of the first eggs laid by the pullets were more strongly related to their age than to their body weight. Additionally, they reveal no association or a very weak association between body and egg weights in the first experiment.

4.3 Natural moult

A natural moult was observed during the present study. As the phenomenon was not anticipated, provision for detailed recording was not made. However, as the moult interfered with the performance of some of the groups under evaluation, as referred in different sections of this thesis, a separate report of its confounding effects on growth and egg production will be made.

The plumage renewal started in early May each year, affecting growing pullets in the first experiment (1996), and laying hens simultaneously in both experiments (1997). The process was not synchronised in time and rather extended for about four months. At the onset of the moulting period, growing pullets were 13-wk old. The laying hens were 36-

wk and 64-wk old and starting the 5th (mid-cycle) and 12th (late-cycle) month of production in the second and first experiment, respectively. The average daylight length during the moulting period was 10.5 hr. Clearly visible de-feathering was observed in all birds with the exception of normal size normal feathered hens (*nana ff Dw-*), but the effects of moult on growth and production were considerably greater among the dwarfs irrespective of their feather coverage.

The effect of juvenile moult on the absolute body weight of Exp. 1 pullets was not clearly visible, as shown in Fig. 4.5. However, a deceleration in the rate of sexual maturing among the dwarfs, measured as body weight relative to the onset body weight, became evident after the 10th week of age (Fig. 4.7), with a resulting 7-day delay in age at first egg, in comparison with their normal size counterparts. As a consequence, early egg production (1-8 weeks) of dwarfs was diminished by 32 % in the first experiment as farther presented in Table 4.17.

Among the Exp. 2 layers (mid-cycle moult), cessation of egg production was observed in 18 % of the dwarf population whereas in just 1 % of the normal birds. In the older group of hens (late-cycle moult), egg laying was interrupted in 12 % and 9 % of the existing dwarfs and non-dwarfs, respectively. At both ages, no normal feathered non-dwarf hen was represented. The mid-cycle moult had a higher depressing effect on the rate of lay of the dwarf hens than that occurred at the end of the productive year (Fig. 4.9), the difference to the normal counterparts being widened by 7.1 % (Exp.2) and 3.3 % (Exp. 1) during the moulting period, as compared with the laying intensity at the onset of the moult. All moulting hens in the second experiment resumed egg production, whereas 29 % of those that halted production in Exp. 1 never recovered. Mean body weight of the various groups of moulting layers was not reduced. However, in the post-moulting period, the weight gain of dwarfs was almost twofold that of normal size hens.

4.4 Productive performance

4.4.1 Egg number

Tables 4.15 to 4.17 present the probability levels and least square means of main and interaction effects on egg number during the whole study. Dietary protein exerted no influence on the number of eggs produced by hen in any of the periods considered. Climatic season was a consistent and significant source of variation during the first laying cycle ($P<0.001$) but had no effect on egg production in the second. In the first eight weeks after housing about 3 more eggs per pullet were produced in the second experiment, whereas in the remaining periods consistently higher production was achieved by hens in the first experiment (14 and 5 eggs/hen in the second and third period, respectively). For the entirety of the 52 weeks, winter layers produced 17 more eggs than those starting lay during the summer. It is interesting to note that precisely similar production was achieved in both experiments during the second cycle, regardless of the different environmental conditions.

During the first laying cycle, no genetic effect other than that caused by the *dw* gene was observed. Dwarf hens laid 60 eggs less than their normal size siblings, which represents a reduction of about 20 %. The absence of a significant interaction with season indicates that approximately the same percentage difference was observed in both experiments. The depressing effect of the dwarfing gene on the number of eggs increased as the laying period progressed from an initial 15 % (1-8 wk) to a final 22 % (31-52 wk). In the second laying cycle, a reducing effect of the *F* gene was observed, with frizzle hens producing approximately 5 eggs less than the fully feathered counterparts ($P<0.05$).

Several interaction effects occurred in part-periods of the first cycle and in the second cycle. Both the *Na* and the *dw* genes interacted with season, the former in the first period and the latter during the whole period of study ($P<0.10$ in the third period). In the pre-peak period, naked neck and dwarf birds in comparison with their respective counterparts produced fewer eggs in the first experiment but similar number in the second, as both genotypes came into lay later. In the remaining part of the cycle, however, differences

between body size groups were greater in the second experiment. The situation was reversed in the second cycle of production, as a wider difference between groups occurred in the first experiment. The diet x *Na* interaction in the second period of the first laying cycle ($P<0.05$) is indicating that the low protein diet reduced production in normal-neck birds (-5 eggs/hen) whereas a slightly larger number of eggs was produced by the naked neck hens fed that type of diet. The interaction between the *Na* and the *F* genes ($P<0.05$) reveals a considerable reduction in the number of eggs produced by hens carrying both genes.

Table 4.18 shows the LS-means by genetic group and percentage deviation from the normal type in each experiment is presented in Fig. 4.10. During the first cycle, it is noticeable the numerical superiority though not significant of the three feather-reduced non-dwarf groups and in particular that of the two naked neck genotypes relative to the control group, which resulted from better performance in the second experiment. Averaged over experiments, the single-gene naked neck birds excelled their normal feathered counterparts by 4 %, corresponding to 10 eggs/hen. Among the dwarfs, both the normal feathered and the single-gene naked neck hens produced approximately 5 eggs/hen plus than the two remaining groups. It is worth noting that the effect of the late sexual maturity in the first experiment of single-gene naked neck dwarfs on early and, as a consequence, on yearly production was overcome by their superior performance in the second experiment. Among the remaining dwarf groups, poorer production and thus higher deviation from the control was observed in the second experiment.

In the second cycle, single-gene naked neck non-dwarf hens produced 9 % more (8 eggs/hen) than normal layers. Conversely, poorer performance than the control group was observed in the combined non-dwarf genotype. Better performance and thus less deviation was observed in the second experiment among the dwarfs.

4.4.2 Laying rate and persistence

Laying rate

Fig. 4.11 illustrates the weekly laying rate (egg production/100 hen day) achieved by normal size and dwarf hens in each experiment, and averaged values by period are presented in Table 4.19. Appreciable differences in the shape of the curves were determined by the season of year, with special relevance to those occurred during the first (1-8 wk) and the second (9-30 wk) parts of the first cycle. Whereas laying intensity in the first experiment increased gradually after the initial peak until the fifth month, when climate was mild, it was seen to decline rather abruptly soon after the peak for equal period in the second experiment. Among the dwarfs, such decline was extended for a further eight weeks. At the end of the fast-growing phase, however, laying rate was higher in the second than in the first experiment. Considerable fluctuations resulting from environmental changes in temperature and relative humidity were noticeable throughout both experiments. It is worth noting the higher fluctuation caused by abrupt rises in temperatures in the laying rate of normal birds as opposed to the more stable production observed in the dwarfs during the summer of Exp. 1 (week 22 to 42).

A specific gene interaction with environment determined another major difference between the curves and hence the production rates of the layers. A comparison between groups within experiments shows marked lowered production in the dwarfs in two particular periods. The first elapsed approximately between weeks 18 and 33 and affected the summer layers, and the second occurred between weeks 44 and 59 involving the winter hens. Such reduced intensity of egg production among dwarfs accompanied an unforced moulting, described in a separate section within this thesis. Differences between body size groups were hence widened in the second and third periods of the first cycle in the second experiment and in the second cycle in the first experiment (Table 4.19). The values in this table are further showing that for the entirety of the first 52-weeks of production, higher rates were observed in the first experiment in both genotypes. Maximum production attained by non-dwarf hens was 97 and 94 eggs/100 hen day in the first and second experiments, respectively, being the correspondent figures for dwarfs 84 % and 82.5 %.

Persistence

Persistence in the first cycle was calculated as the time at which 60 % of the yearly production was attained and as the ratio between the number of eggs produced during the third and the second laying periods (Tables 4.20 and 4.21). Regardless of the method used to measure this trait, it was influenced by the season of year ($P<0.001$). Resulting from the specific pattern of production over time previously described, higher persistence was observed in the second than in the first experiment, as egg production from 31-52 weeks almost equalled that attained from 9-30 weeks. However, the difference resulted mainly from the lowered production attained by the summer layers in the second period of the cycle. On the other scale, summer birds reached 60 % of the yearly production approximately one week later than their winter replicates. Significantly lower ($P<0.001$) persistence of dwarfs was observed using the first but not the second method of measurement. Nonetheless, both methods indicate that differences between the body size groups were higher in the first experiment (Table 4.22).

The persistence of production throughout the second cycle was measured relatively to the previous period (31-52 wk), with equivalent duration. Egg production was seen to be considerably more persistent in the second experiment in comparison with the first ($P<0.001$), and the ratio was equal to that measured in the first cycle. Dwarf birds showed an outstanding persistence in the second experiment ($P<0.001$), since they laid precisely the same number of eggs during the second cycle as in the last 5.5 months of the first year (Table 4.22).

Table 4.23 shows that, averaged over experiments, P(60) was fairly homogenous among the feathering types within body size groups. Dwarf birds attained 60 % of the yearly production about one week before than their non-dwarf counterparts. However, only the persistence of normal feathered and frizzle dwarfs was seen to be statistically different from the control group ($P<0.05$). The ratio yielded similar values between the groups both in the first and the second cycle. However, it is worth noting the consistently high persistence of naked neck non-dwarf hens in both cycles.

4.4.3 Egg weight

Tables 4.24 to 4.26 show the probability values and LS-means of main and interaction effects on egg weight. Eggs produced in the second experiment were on average 2.4 g lighter than those laid in the first experiment in both cycles studied (P<0.001). Yet, in the last part of the first cycle egg size was similar between experiments. The trait was not influenced by the dietary protein, but the interaction with season observed throughout the first cycle (P<0.05) shows that eggs laid by hens fed the HP diet were heavier than those produced by birds under the LP regime in Exp. 2 but not in Exp. 1.

On overall terms, neither the *Na* nor the *F* gene influenced egg weight. However, the first gene interacted with diet (P<0.05) and the second with season (P<0.05). Hens carrying the naked neck gene produced heavier eggs when fed the LP diet in almost all periods considered, whereas the lower protein content of the diet was associated with decreased egg weight among their counterparts with normal neck. Frizzle layers in comparison with their normal counterparts produced heavier eggs only in the first experiment.

The dwarfing gene caused an average reduction of 9 % in the first and 7 % in the second cycle (P<0.001). The interaction between the *dw* gene and the season reveals that egg weight differences determined by the body size of the layers were not uniform between experiments. Differences were lower in the first experiment as compared with the second, reaching significance in the first and third periods of the first cycle (P<0.05).

On average over experiments, no major differences on egg weight were observed among feathering types within body size groups in both cycles (Table 4.27). However, the values in Fig. 4.12 indicate that, in the first cycle of the first experiment, egg weight of feather reduced non-dwarf groups was approximately 3 % higher than the normal type. During the second cycle, higher egg weight was still observed in the two frizzle non-dwarf genotypes in the first experiment. Greater deviation of dwarf birds from the normal type was observed in the second experiment.

Time trends of environmental and genetic effects on egg weight are depicted in Fig. 4.13 and the mathematical parameters for the description of the curves are presented in Table

4.28. Fluctuations induced by the prevailing environmental conditions were observed throughout the period of study. Response of body size groups to seasonal variations of climate was fairly uniform in the second experiment, as the respective curves evolved parallel, with similar rate of growth. Conversely, appreciable differences between the genotypes were observed in the first experiment, being worth noting the higher fluctuations occurred in the non-dwarfs, and the lower goodness of fit of the equation. As a result, for the entirety of the cycle, egg weight increase over time was both smoother and higher in the dwarfs in comparison with the normal birds, as also revealed by the higher rate of growth observed in the former group of layers.

4.4.4 Egg mass

Probability levels and least squares means of main and interaction effects on egg mass are presented in Tables 4.29 to 4.31. Higher egg mass was produced in the first than in the second experiment in all periods with the exception of the first ($P<0.05$). None of the feather reducing genes influenced egg mass, but the *Na* gene consistently interacted with diet in the last two periods of the first cycle ($P<0.05$). Naked neck birds produced higher mass of eggs (+0.3 kg/hen) when fed the low protein diet whereas their fully feathered counterparts produced most (+0.7 kg/hen) under the high protein regimen. The *Na* gene also interacted with season during the first two months of production, since a significantly lower egg mass was produced by hens carrying this gene in the first experiment ($P<0.05$). In the second period, higher production was observed in the naked neck non-dwarfs whereas lower in the naked neck dwarfs in comparison with their respective fully feathered counterparts ($P<0.05$). The *Na* x *F* interaction observed during the second cycle ($P<0.05$) shows that production of single-gene naked neck birds was higher (+0.4 kg/hen) than their normal feathered siblings, while hens carrying both the naked neck and frizzle genes had lower egg mass (-0.2 kg/hen) than the single-gene frizzle layers.

At the end of the first cycle, dwarfs had produced less 5 kg of egg mass per hen than the normal layers ($P<0.001$), corresponding to a 27 % reduction. In the following period (LC-II) the reduction was further increased to 28 %. For the entirety of first cycle, dwarf

hens produced a lower amount of egg mass in the second experiment comparatively with the first, whereas production among the normal hens was similar in both experiments, as revealed by the season x *dw* interaction (P<0.01).

The analysis by genetic group (Table 4.32 and Fig. 4.14) shows a slight advantage of feather-reduced non-dwarf birds in the first experiment but not in the second. Averaged over experiments the naked neck genotype excelled the remaining groups in both cycles, the difference to the control being statistically significant from 31 weeks onwards (P<0.05). Among the dwarfs, egg mass production of feather-reduced groups followed closely that of the normal feathered siblings, it being worth noting that the lowest production was attained by the three-gene combination group.

4.4.5 Biological efficiency and productivity

Both daily egg mass and total egg numbers were expressed in terms of metabolic body weight and the results presented in Tables 4.33 to 4.35.

During the first year, lower egg mass (P<0.001) but similar number of eggs per kg $^{0.75}$ were produced in the second experiment as compared with the first. The *Na* gene was associated with higher biological efficiency and higher productivity relatively to birds with normal neck (P<0.05). Dwarf birds produced a similar amount of egg mass but a significantly greater number of eggs per kg $^{0.75}$ than their normal counterparts (P<0.001). The *Na* x diet interaction for biological efficiency (P<0.01) shows that the normal birds produced a lower mass of eggs when fed the LP diet, whereas higher production was achieved by naked hens fed the same diet. The interaction between the *dw* gene and season for the same trait (P<0.001) indicates that dwarf hens showed better biological efficiency than their normal counterparts in the first experiment but poorer in the second. The equivalent interaction for productivity (P<0.01) shows that, although dwarfs produced a greater number of eggs per metabolic weight than normal hens in both experiments, the latter group showed better productivity in the second experiment while dwarfs attained higher productivity in the first.

During the second cycle of production, equivalent egg mass per $kg^{0.75}$ was produced in both experiments, whereas higher productivity occurred in the second experiment ($P<0.05$). Higher productivity was still observed in dwarf hens during this period ($P<0.01$). An interaction between the *Na* and the *F* genes occurred for both traits ($P<0.05$). They reveal higher biological efficiency and productivity of single-gene naked neck hens, while lower in birds carrying both genes. In overall terms, biological efficiency declined 8 % from the first to the second experiment, and productivity was seen to reduce by 15 %.

Table 4.36 presents the LS-means in the genetic groups and Fig. 4.15 show its breakdown by experiment as percentage difference to the normal type. It is worth noting that, among the non-dwarfs, single-gene naked neck layers consistently excelled normal hens, though by a small margin, both in efficiency and productivity. Dwarf hens showed higher biological efficiency than the control birds in the first experiment, but lower in the second. Conversely, their productivity was higher in both experiments and cycles.

4.4.6 Feed intake per kg $^{0.75}$

Feed intake was corrected for body weight differences of birds and results are presented in Tables 4.37 to 4.39. Dietary protein influenced feed consumption only in the second cycle, a period in which hens fed the low protein consumed 4 % more than their counterparts under the high protein regime ($P<0.01$). Conversely, season affected feed intake only in the first cycle, as 3 % more feed was needed per unit of metabolic weight in the first experiment ($P<0.001$). Feed intake was lower in periods with higher temperatures, with differences between experiments decreasing as the laying cycle progressed.

Hens carrying either the *Na* or the *F* gene consumed significantly more feed per unit of metabolic weight than their normal feathered counterparts in both cycles studied ($P<0.001$). On average terms, dwarf hens required less feed per unit of metabolic weight in both cycles than their normal siblings ($P<0.01$). However, the consistent S x *dw* interaction occurred ($P<0.001$) shows that for most of the first experiment, dwarfs

consumed slightly more than normal birds whereas considerably less during the whole second experiment.

Two other interactions occurred during the second period of the first production year. The D x S interaction ($P<0.05$) reveals that consumption of the LP in comparison with the HP diet was higher in the first experiment though lower in the second. The S x *Na* interaction ($P<0.05$) indicates that the difference in feed intake between naked neck and normal neck birds in the first experiment was two-fold that in the second.

Table 4.40 presents the LS-means of feed intake in the genetic groups evaluated and Fig. 4.16 shows the values as percentage difference from the normal type in each experiment. It is noticeable the higher consumption of the feather-reduced genotypes in comparison with the normal-feathered ones within each body size group, with special emphasis to birds carrying both the naked neck and frizzle genes. It is also worth to note that normal feathered dwarfs were the only group showing consistently lower feed consumption per unit of metabolic weight than the control group in both experiments and cycles.

4.4.7 Feed efficiency

Climatic season but not diet influenced the efficiency of feed utilisation throughout the first production year ($P<0.001$), as shown in Tables 4.41 and 4.42. Efficiency was higher in the cycle beginning in the coldest months of the year (Exp. 1) than in that initiated during the summer (Exp. 2). Extreme differences were observed in the first two months of production, when feed consumed per unit of egg mass was 1.5 times higher in the first than in the second experiment, resulting from reduced egg mass. The trait was maximised in the following period within each experiment. A similar amount of feed was needed per unit of egg mass during the second cycle of production in both experiments. A comparison between cycles shows that the efficiency of food utilisation decreased on average 9 % in the second cycle.

The effect of the *Na* gene on this trait was observed only in the first two months of production, with naked neck birds being less efficient than their fully feathered

counterparts (P<0.01). However, the interaction with season (P<0.01) indicates that it resulted from the considerably lower efficiency associated with reduced egg mass in the first experiment, as they started laying later (Table 4.43). Naked neck hens were more efficient when fed the low protein than the high dietary protein, whereas the reverse was observed in birds with normal feathered neck. However, significance was reached (P<0.01) only when the 52-wk period is considered. Lower efficiency was also observed in hens carrying the *F*-gene during both the first and the second cycle of production (P<0.01). Moreover, in the second cycle as compared with the first, efficiency of frizzle birds substantially decreased (+ 12 % feed per unit of egg mass). The combination of both the *Na*- and *F*-genes worsened the efficiency of feed utilisation after the 30th week of production, affecting both cycles (P<0.05).

Dwarf birds needed less feed than their non-dwarf counterparts to produce one unit of egg mass in the first cycle (P=0.056). The effect was not consistent throughout each experiment, as revealed by the interaction between the dwarf gene and season. Dwarfs in comparison with normal hens had lower efficiency in the first two months of the first experiment but higher in the same period of the second experiment. The situation was reversed in the following period.

The results for the genetic groups are presented in Table 4.44 and percentage differences to the control are plotted in Fig. 4.17. It is worth noting that, within each body size group naked neck frizzle birds had the poorest feed efficiency of all groups, and that only naked neck non-dwarfs and normal feathered dwarfs showed consistently better efficiency in comparison with the control type in both cycles studied

4.4.8 Body weight gain

Body weight gain was 10 % lower in hens fed the low protein diet during the first production year (P<0.01), the effect being visible from the second month onwards (Tables 4.45 and 4.46). Moreover, hens fed the lower dietary protein lost weight in the first experiment, as revealed by the diet x season interaction (P<0.05) shown in Table 4.47. There were significant seasonal effects (P<0.01) on body weight gain in all but one

of the periods studied, the exception being the last part of the first cycle. Higher temperatures were associated with lower gains, with greater differences occurring in the first 30 weeks of laying. Over the 52-wk period, hens starting production during the hottest season (Exp. 2) showed greater increase in body weight than those coming into lay in winter (Exp. 1). The increase represented 40 % and 34 % of the initial weight at housing, respectively.

Weight gain of hens carrying the *Na* gene was consistently lower when the whole cycles were considered ($P<0.05$). Significant though converse interactions between this gene and the environment ($P<0.05$) occurred after the 30th week. They reveal similar or greater increase in body weight of naked neck layers in periods with higher temperature and lower growth in periods with milder climate.

Body weight development of hens carrying the *F* gene was very low and significantly different from that of normal counterparts in the last part of the first cycle and in the second cycle. In the former period, this was attributed exclusively to single-gene frizzle hens, since the reducing effect on weight gain was overcome when the *F* and the *Na* gene were associated, as shown by the respective interaction. In the latter period, non-dwarf hens, which lost weight, were responsible for the decreased gain observed among the frizzle birds, according to the interaction between the *F* and the *dw* gene.

Weight gain of dwarf hens was substantially lower in the first cycle ($P<0.001$), but almost two-fold that of the normal birds in the second cycle ($P<0.05$). In relative terms to the initial body weight at housing, body weight increased 40 % in the normal hens and 37 % in dwarfs by the end of the first year, and 41 % in both size groups by week 76 of production. A *dw* x season interaction was observed after the 9th week ($P<0.05$), showing that an extremely low increase in weight (9-30 wk) or a weight loss (31-52 wk) occurred in dwarfs in the experiment with higher prevailing temperatures.

In Table 4.48 are presented the LS-means for body weight gain in the different genetic groups. Numerically higher gains occurred in normal feathered birds within each body

size group, either in the first or the second cycle. Furthermore, in the latter period, frizzle and naked neck frizzle non-dwarfs halted growth and lost weight, respectively.

Body weight gain of layers over time is plotted in Fig. 4.18, with pooled data from normal and dwarf birds. Seasonal influence of climate was clearly visible throughout, as lower gains occurred in periods when temperature was higher.

4.4.9 Liveability

Probability levels and LS-means of main and interaction effects on liveability are presented in Tables 4.49 and 4.50. Seasonal effects were seen during the first cycle of production ($P<0.001$), as higher mortality was observed in the first experiment (13.5 %) comparatively with the second (2.8 %). The season x *dw* locus interaction ($P<0.05$) observed in that cycle indicates that significantly more non-dwarf than dwarf birds died during the first experiment whereas similar mortality occurred in the second. Such differences are mainly attributable to the number of birds that died due to heat stress (HS1, 73 % nondwarfs and 27 % dwarfs). Survivability of naked neck hens was significantly higher ($P<0.05$) in the second cycle of production in both experiments.

Despite the numerical differences in mortality of the various genetic groups, no statistical difference was observed to the control type (Table 4.51). When the whole period of study was considered (76 weeks), survivability of the different dwarf genotypes was, on average, 4 % higher than the normal reciprocals.

Acute heat stress was responsible for 55 % of the deaths in Exp. 1 and 36 % in Exp. 2 during the first laying year and for 41 % of the mortality observed in the latter experiment during the second cycle. High mortality occurred in three particular days, as indicated in Fig. 4.19, as a result of a combined effect of extremely high temperature, above 39 °C, and relative humidity below 50 %. Prolapsed oviducts were the next main cause of death, whose incidence in the heavier Exp.1 hens was almost two-fold that of their counterparts in the second experiment.

4.4.10 Egg quality

Probability values and LS-means of main and interaction effects on selected egg quality traits are presented in Tables 4.53 to 4.55. On average terms, the weight of the yolk per unit of egg increased as the hen aged ($P<0.001$), but differences occurred between experiments within ages, as revealed by the age x season interaction. At the early stage of the laying cycle (28-wk of age), the proportion of yolk was similar in both experiments and seemed independent of the environmental conditions prevailing in each one. However, at both 40 and 64 weeks of age, a comparison between experiments shows lowered yolk proportion in the periods where temperature was elevated (40 wk in Exp. 2 and 64 wk in Exp. 1). This interaction additionally indicates that, in the first experiment the increase in the weight of the whole egg between 40- and 64-wk (data not shown) was done at the expense of an increase in albumen, as the proportion of yolk remained unchanged. The normal hens but not the dwarfs contributed to this occurrence, as revealed by the second and third order interactions between age, season and the *dw* locus ($P<0.05$). Hens carrying the *Na* gene showed higher proportion of yolk in the egg than their fully feathered counterparts ($P<0.05$) and the *Na* x *F* interaction indicates that the trait was further increased when both genes were associated ($P<0.05$).

Seasonal variation throughout ages was observed for albumen height, that was on average slightly higher at 40-wk than at 28-wk and considerably lower at 64-wk ($P<0.001$). The values given by the age x season interaction ($P<0.001$) show an inverse relation of the trait with the environmental temperature at each age in each experiment. The age x *dw* locus interaction ($P<0.001$) indicates a higher persistence of albumen quality at the older age in the dwarfs as opposed to a higher decrease of the trait among the normal hens. Naked neck hens produced eggs with poorer albumen quality than their counterparts ($P<0.05$).

Both the breaking strength and the weight per unit of egg of the shell decreased though its thickness increased as the hen aged ($P<0.001$). The last two traits varied inversely with the environmental temperature prevailing at each age within experiment ($P<0.001$). The resistance of the shell to breakage seemed independent of climatic fluctuation, yet a greater decline was observed between 40- and 64-wk of age in the second experiment

(P<0.01). Averaged over time, eggs produced in Exp. 2 showed lower proportion of shells and decreased breaking strength (P<0.01). The dwarfing gene was associated with greater proportion (P<0.001) and higher strength of the shell (P<0.05), and an interaction between age and the *dw* locus shows that dwarfs maintained the proportion of shell in the egg at older ages whereas it declined among the normal size hens (P<0.01).

The protein content of the diet affected neither the interior nor the exterior quality of the eggs, although the height of the albumen was slightly higher and the breaking strength slightly lower in hens fed the low protein diet.

Egg quality was very homogeneous among the different genetic groups, and no differences were observed to the control type (Table 4.56).

4.5 The penalties of heat stress to production and survival

The vulnerability of the birds to weather was established in previous sections of this work, since direct and indirect effects of environmental temperatures above the thermoneutral zone influenced their performance and survival. The production function and the liveability of birds exposed to thermal environments can be quantitatively related to a stress index in which the two main physical environmental determinants, temperature and humidity, are expressed.

Temperature-humidity index (THI) was calculated for the whole laying period and values were related to different traits, in order to categorise the penalties to performance and survival. Decreases in egg production caused by environmental factors above the «normal» physiological decline were considered as being the differences to the slope of a regression equation applied beyond the peak production (dwarfs in Exp. 2 were excluded due to the additional confounding effects of moult). Decreases in egg weight and feed consumption were directly estimated as percentage differences to the preceding period. Safety categories and proposed minimum precautions were also considered. Results are presented in Table 4.56.

It is worth noting that egg production was the most responsive trait to the stressful effects of heat and humidity, as losses of up to 5 % were observed above a THI value of 79, corresponding to maximum room temperature above 28 °C. Appreciable decrease in egg weight and feed intake occurred only when the temperature-humidity index was 83 or higher, which corresponds to maximum temperatures above 31 °C. Extreme effects of heat with severe losses in production and occurrence of deaths were observed when THI reached values of 86 or higher, resulting from maximum temperatures above 37 °C. Severe mortality occurred when a hot spell was combined with relative humidity below 50 %.

4.6 Economic analysis

4.6.1 Feed conversion

Tables 4.57 and 4.58 present the probabilities and LS-means of main effects on feed conversion. Only the influence of the *F* and *dw* genes was observed on this trait, since exactly the same amount of feed per dozen eggs was required in each diet or experiment. Approximately 3 % more feed in the first cycle and 10 % in the second was needed by frizzle hens to produce one dozen eggs in comparison with normal birds ($P<0.01$). Dwarf layers, on its turn, required 10 % and 7 % less feed per dozen eggs than the non-dwarf counterparts in the first ($P<0.001$) and second ($P<0.01$) cycle, respectively. The season x *dw* interaction occurred in the second cycle ($P<0.05$) shows similar feed conversion in either normal or dwarf hens in the first experiment (2.0 kg/dz egg), whereas 14 % less feed per dozen eggs was required by dwarfs in the second experiment (1.8 kg in *dw*-; 2.1 kg in *Dw*-). Feed conversion declined 18 % in the second cycle in comparison with the first, as 300 g more of feed were needed to produce each dozen eggs.

Table 4.59 shows a great deal of homogeneity between the different genetic groups and the normal type. However, it is worth noting that naked neck frizzle birds in both body size groups required the largest amount of feed to produce one dozen eggs.

4.6.2 Egg size classification

Table 4.60 shows the size classification of marketable eggs by body size of the hens in each experiment and laying cycle. A different distribution of egg sizes was observed in each of those entities. The experiment starting in winter time yielded a greater percentage of the larger eggs in both normal and dwarf groups (+ 10% above 54.3 g). Conversely, in the second experiment, 1.5 and 3 times more small and medium eggs were produced among the dwarfs and non-dwarfs, respectively.

In the second cycle, most of the eggs produced by normal hens were classified as extra-large and jumbo. A greater differentiation between experiments, however, was observed among the dwarfs, as 1.5 times more eggs of that grade were produced in the first experiment.

A comparison between cycles shows a higher increase in egg size with age of the hens in the dwarfs, especially in the first experiment. The proportion of very large eggs in this genotype was three- and two-fold greater in the first and second experiment, respectively, whereas just 1.5 times among the normal size hens in both experiments.

4.6.3 Economic evaluation of the genetic groups

In the present study, input variables such as the genetics of birds, quantity and quality of feed, and environmental conditions were evaluated, and several output variables were measured. The exercise of calculating the profitability of the eight different genotypes under study was done from the point of view of a prospective farmer producing either for formal urban or informal peri-urban market in Maputo. According to this approach, the analysis was based on different scenarios contemplating the following alternatives:

a) differentiated egg prices based either on potential grading system or unclassified eggs;
b) the potential extra revenue derived from the additional value of feather-reduced birds at the end of their productive life (LC I);

c) the potential extra benefit of a higher stock density per unit of area resulting from the use of smaller birds.

The analysis was based on the gross margin principle, i.e. total income less allocated costs. For the purpose of this comparative exercise, only the net cost of the hen (cost of replacement pullet minus the value of the spent hen) and the feed cost were included, as all the remaining costs of the enterprise were considered independent of the bird's genotype and constant (*ceteris paribus* condition). Selected economic indicators are presented in Table 4.61, and a comparative evaluation is contained in Table 4.62, both deriving from the values presented in Annexes 2 to 6.

Economic indicators

Contribution margin measures the percentage of the gross income that is left by allocated cost to cover all the remaining production costs (Table 4.61). A higher contribution margin was given by dwarfs, resulting from proportionally lower feed costs as well as lower cost of the replacement pullet in comparison with normal hens. Naked neck frizzle groups, either non-dwarf or dwarf, presented the lowest values. Lower feed cost in dwarfs also determined a wider margin of the break-even over the current feed price and a narrower margin of break-even over current egg price. In physical terms, the break-even output of dwarfs in comparison with normal hens corresponded to a slightly lower proportion of the annual production.

Extra revenue from the sale of feather-reduced spent hens at differentiated prices might be obtained by the farmer in peri-urban markets. The impact on gross margin per bird would be higher in the case of hens carrying the frizzle gene as this genotype is preferred for healing traditional ceremonies. Non-dwarf hens would be favoured in the event of eggs being graded and prices differentiated accordingly. The gross margin of the farmer could thus be increased by approximately 40 % if non-dwarf hens were used, whereas only 9 % if eggs were produced by dwarfs.

On average terms, the contribution margin of feed cost in the second cycle decreased 25 % relative to the first year. This figure was the combined result of a 16 % reduction in

the revenue from egg sale and a 4 % increase in the feed cost. A straight second cycle, in the conditions of the present study, would be of interest to the farmer if the profits were higher than those obtained with a new stock in equivalent time period. The profitability of a straight second cycle of production was then assessed. The upper limit (in time units) would correspond to the point where the marginal revenue obtained equals the marginal cost. The marginal cost was the proportional gross margin foregone for not investing the revenue from the spent hen in a point-of-lay pullet (in the present case 40 %). An example is shown in Fig. 4.20 for the control type (*nana ff Dw-*). It is worth noting from Table 4.61 that the lowest limit was associated with naked neck frizzle and the highest with naked neck hens, both non-dwarfs. A farmer would be able to extend the laying period for about 4 months, beyond the first year, when using the latter genotype, but would not proceed to a second cycle if the former genotype was to be considered. The remaining genetic groups would allow extended production for periods ranging from 1 to 3.5 months beyond the first cycle.

Normal feathered non-dwarf hens achieved exactly the same gross margin per hen housed in both experiments, as lower mortality compensated for reduced production in the second experiment. Financial results of naked neck birds either dwarf and non-dwarf were much superior in the second experiment, due not only to lower reduction in marketable production but also and fundamentally to 0 % mortality observed in both groups in this hotter experiment. It is also worth noting the effect of moult on lowering the gross margin of normal feathered, single and combined frizzle dwarf hens in the second experiment

Comparative financial analysis

Selected financial parameters of the different genetic groups were compared with the control type in Table 4.62. Among the non-dwarf groups, only single gene naked neck hens excelled the normal type of birds, as they obtained a slightly higher margin over feed costs per surviving hen and a 6 % higher gross margin per hen housed. The latter figure derived from 14 % higher gross profitability in the second experiment and similar results in the first. Among the dwarfs, the best financial return was achieved by normal feathered, closely followed by naked neck birds. Their gross margin on a hen-housed

basis was, respectively, 15 and 9 % higher than that of a normal hen. In spite of their much lower feed cost per hen, however, these dwarf groups could not compete with the control bird in terms of margin over feed cost, given the current relation between the prices of feed and eggs. Within each body size group, single gene and combined frizzle birds showed inferior economic performance in comparison with the normal ones.

As mentioned earlier in this work, body weight of dwarfs was approximately 30 % lower than that of non-dwarf birds, which would allow a higher population density to be used per unit of area. Considering a proportional increase in the bird density, i.e. 1.3 dwarfs *versus* 1.0 non-dwarf, the profitability per unit of housing area could be as much as 49 % higher in comparison with the normal type.

TABLES & FIGURES

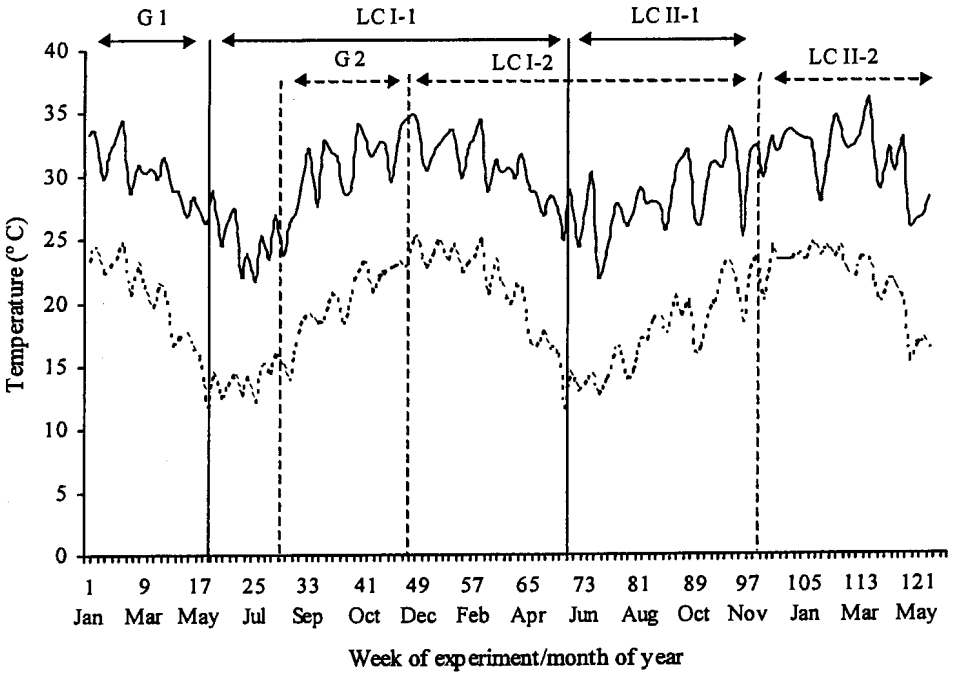


Figure 4.1 - Room maximum (—) and minimum (---) temperatures during the study: (G1 and G2) growing in Exp.1 and Exp.2; (LCI-1 and LCI-2) first laying cycle in Exp.1 and Exp.2; (LCII-1 and LCII-2) second laying cycle in Exp.1 and Exp.2

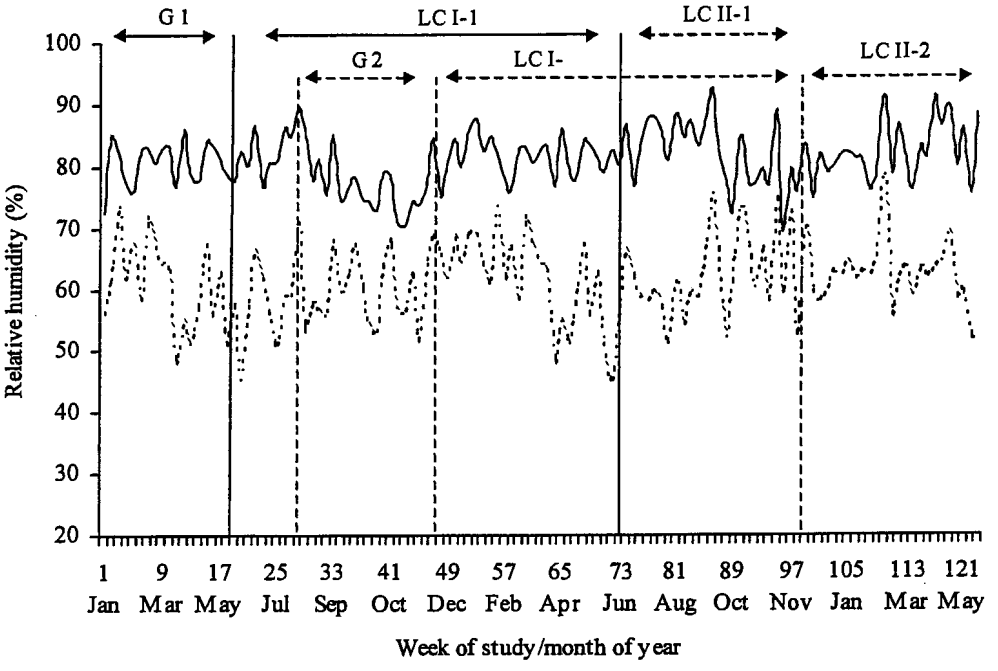


Figure 4.2 - Room maximum (—) and minimum (---) relative humidity during the study: (G1 and G2) growing in Exp.1 and Exp.2; (LCI-1 and LCI-2) first laying cycle in Exp.1 and Exp.2; (LCII-1 and LCII-2) second laying cycle in Exp.1 and Exp.2

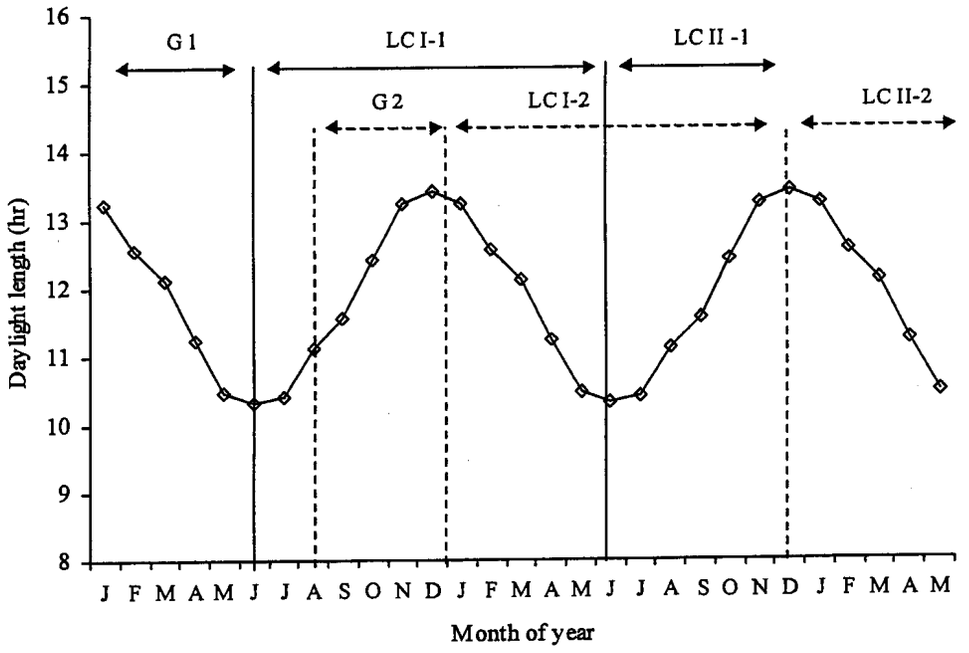


Figure 4.3 - Monthly average daylight length (hr) during the study: (G1 and G2) growing in Exp.1 and Exp.2; (LCI-1 and LCI-2) first laying cycle in Exp.1 and Exp.2; (LCII-1 and LCII-2) second laying cycle in Exp.1 and Exp.2

Table 4.1
Climatic conditions during the laying phase

	LC I				LC II			
	1-8 wk		9-30 wk		31-52 wk		53-76 wk	
	Exp.1 Jul-Aug	Exp. 2 Dec-Jan	Exp.1 Sep-Jan	Exp. 2 Feb-Jun	Exp.1 Feb-Jun	Exp. 2 Jul-Nov	Exp.1 Jul-Dec	Exp. 2 Dec-May
Ta [1]								
Max	25.4	32.5	32.0	27.8	29.0	29.8	29.2	31.4
Min	15.1	23.8	22.0	16.7	18.3	19.9	19.2	21.8
Avg	20.7	28.3	27.0	22.2	23.5	24.8	24.2	26.6
RH [2]								
Max	82.5	82.1	78.2	82.4	81.3	81.0	81.8	81.9
Min	58.0	66.3	62.8	59.0	60.5	62.5	61.9	61.8
Avg	70.3	74.2	70.5	70.7	70.9	71.8	71.9	71.9

[1] Ta = room temperature (°C); [2] RH = room relative humidity (%)

Table 4.2
Probabilities of main and interaction effects on body weight of growing pullets

Source of Variation	Body weight (g)	
	8 wk	18 wk
Season (S)	**<0.001**	**<0.001**
Na locus	0.450	0.979
F locus	0.329	**0.016**
dw locus	**<0.001**	**<0.001**
S x *Na*	**0.015**	0.115
S x *F*	0.151	0.659
S x *dw*	0.307	**0.014**
Na x *F*	0.126	0.246
Na x *dw*	0.132	0.276
F x *dw*	0.553	0.980

Table 4.3
LS-means of main effects on body weight of growing pullets

Factor		Body weight (g)	
		8 wk	18 wk
	μ	524.4	1345
	SE	2.9	7
Season	Exp. 1	505.8	1372
	Exp. 2	542.9	1319
Na	*nana*	522.2	1345
locus	*Nana*	526.6	1345
F	*ff*	527.2	1361
locus	*Ff*	521.6	1329
dw	*Dw-*	623.0	1615
locus	*dw-*	425.8	1076

Table 4.4

LS-means of interaction effects on body weight of growing pullets

Season x *Na* locus			**Season x *dw* locus**		
	8 wk (μ=524.4)			18 wk (μ=1345)	
	nana	*Nana*		*Dw-*	*dw-*
Exp.1	510.7	501.0	Exp.1	1658	1086
Exp.2	533.7	552.2	Exp.2	1572	1066

Table 4.5

LS-means of body weight of growing pullets in the genetic groups

Body size type	Feathering Type	Body weight (g) 8 wk	18 wk
	nana ff	623.5	1634
	Nana ff	631.6	1628
Dw-	*nana Ff*	609.5	1582
	Nana Ff	627.4	1616
	nana ff	435.4 *	1105 *
	Nana ff	418.3 *	1079 *
dw-	*nana Ff*	420.4 *	1061 *
	Nana Ff	428.9 *	1057 *

* Significantly different (P<0.05) from the control *nana ff Dw-*

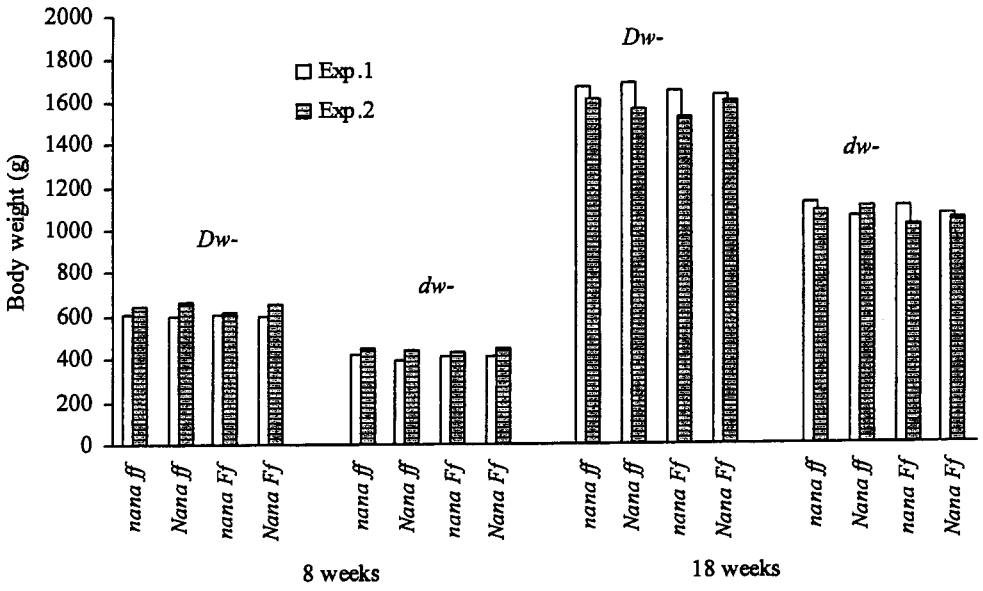


Figure 4.4 - Body weight of growing pullets by genetic group and experiment.

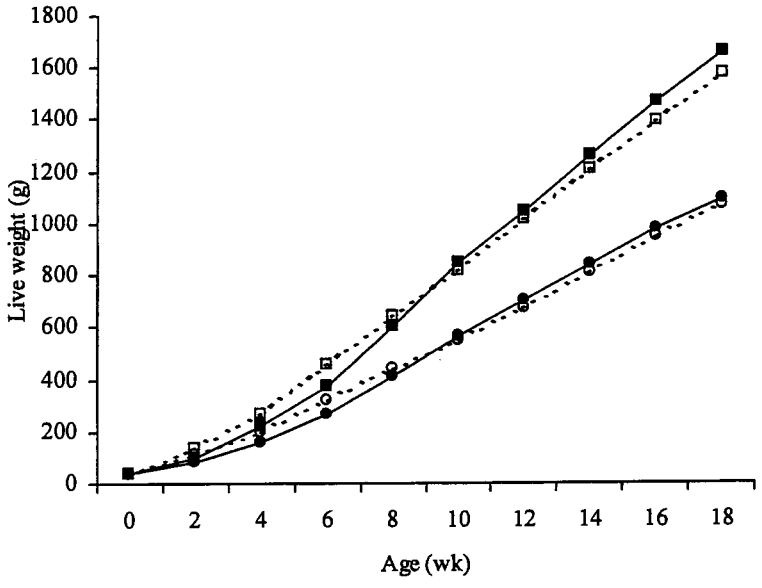
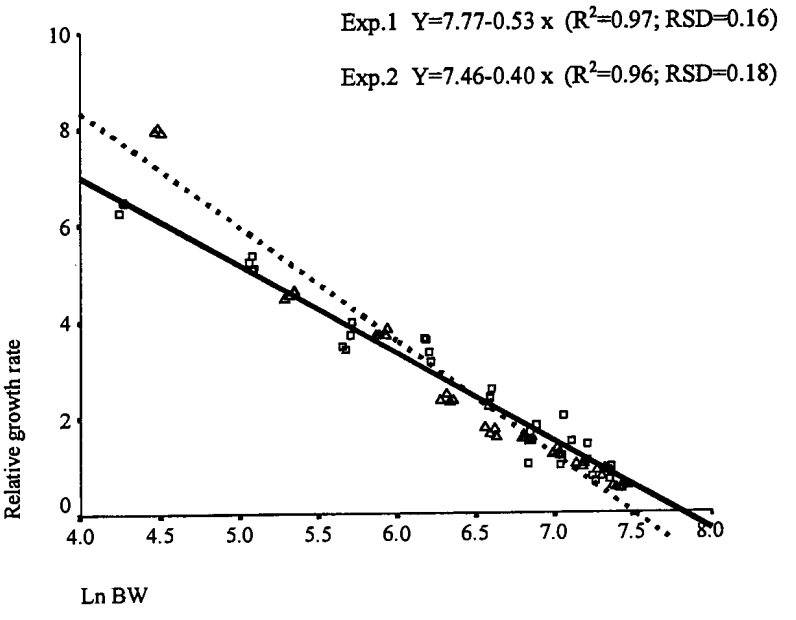
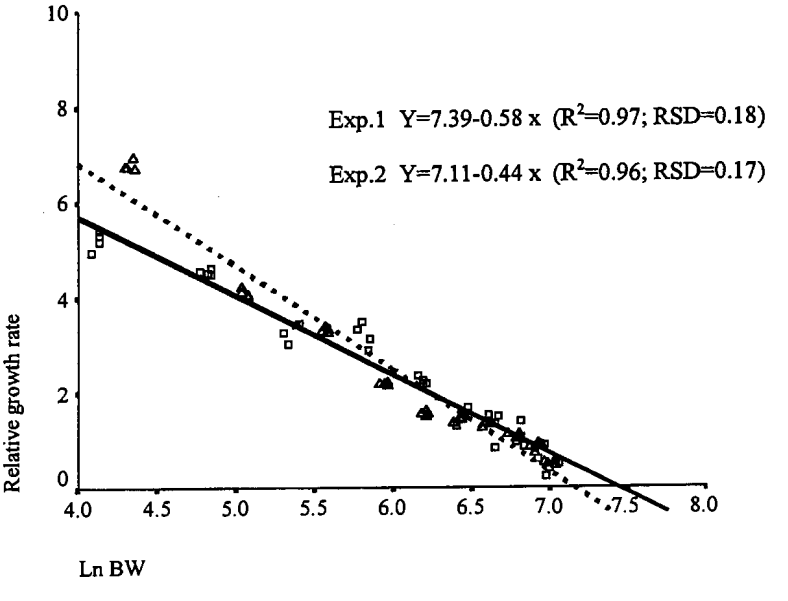


Figure 4.5 - Body weight curve of growing pullets by body size group and experiment (normal size: ■—■ Exp. 1, □----□ Exp. 2; dwarf: ●—● Exp. 1, ○---○ Exp. 2).



(i) Normal



(ii) Dwarf

Fig. 4.6 - Relative growth rate of normal and dwarf pullets plotted against the natural log (Ln) of body weight and regression lines (Exp. 1 □ —; Exp. 2 Δ ----)

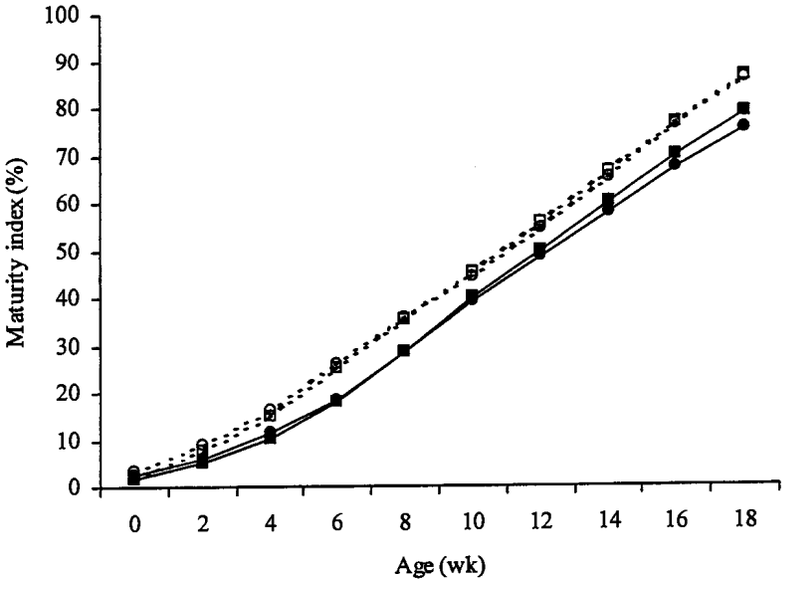


Figure 4.7 - Growth pattern of normal and dwarf pullets when body weight was expressed as % of body weight at sexual maturity (maturity index)
(normal size: ■—■ Exp. 1, □----□ Exp. 2; dwarf: ●—● Exp. 1, ○----○ Exp. 2).

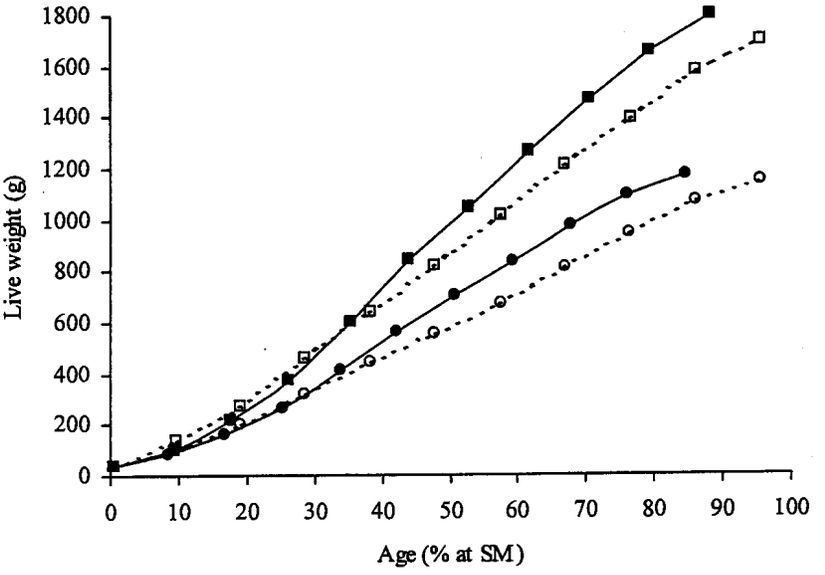


Figure 4.8 - Growth pattern of normal and dwarf pullets when chronological age was expressed as % of age at sexual maturity
(normal size: ■—■ Exp. 1, □----□ Exp. 2; dwarf: ●—● Exp. 1, ○----○ Exp. 2).

Table 4.6

Probabilities of main and interaction effects on traits at sexual maturity

Source of variation	Traits at sexual maturity		
	Age (d)	Body weight (g)	Egg weight (g)
Diet (D)	0.079	0.644	0.687
Season (S)	**<0.001**	**<0.001**	**<0.001**
Na locus	0.312	0.590	0.794
F locus	0.869	**0.032**	0.396
dw locus	**<0.001**	**<0.001**	**<0.001**
D x S	0.723	0.300	0.117
D x *Na*	0.403	0.439	0.193
D x *F*	0.294	0.817	**0.042**
D x *dw*	0.798	0.467	0.106
S x *Na*	**0.001**	0.465	0.797
S x *F*	0.270	0.833	0.805
S x *dw*	**<0.001**	0.640	**<0.001**
Na x *F*	0.129	0.253	0.081
Na x *dw*	0.074	0.809	0.057
F x *dw*	0.339	0.396	0.748

Table 4.7

LS-means of main effects on traits at sexual maturity

Factor		Traits at sexual maturity		
		Age (d)	Body weight (g)	Egg weight (g)
	μ	155.6	1688	46.2
	SE	0.5	8	0.2
Diet	HP	156.4	1682	46.1
	LP	154.7	1693	46.3
Season	Exp. 1	163.8	1814	49.0
	Exp. 2	147.3	1562	43.5
Na locus	*nana*	155.1	1692	46.3
	Nana	156.0	1683	46.2
F locus	*ff*	155.6	1706	46.4
	Ff	155.5	1669	46.0
dw locus	*Dw-*	153.7	2006	47.6
	dw-	157.4	1369	44.8

Table 4.8

LS-means of interaction effects on age at sexual maturity (d) and initial egg weight (g)

Season x *dw* locus				
	Age (μ=155.6)		Egg weight (μ=46.2)	
	Dw-	*dw-*	*Dw-*	*dw-*
Exp.1	160.3	167.4	49.6	48.3
Exp.2	147.0	147.6	45.7	41.2

Season x *Na* locus		
	Age (μ=155.6)	
	nana	*Nana*
Exp.1	161.8	165.9
Exp.2	148.4	146.2

Diet x *F* locus		
	Egg weight (μ=46.2)	
	ff	*Ff*
HP	46.7	45.6
LP	46.1	46.5

Table 4.9

LS-means of traits at sexual maturity in the genetic groups

		Traits at sexual maturity		
Body size type	Feathering type	Age (d)	Body weight (g)	Egg weight (g)
	nana ff	153.7	2017	47.8
	Nana ff	154.7	2024	47.9
Dw-	*nana Ff*	154.5	1999	48.3
	Nana Ff	152.0	1985	46.5
	nana ff	155.2	1415 *	44.4 *
	Nana ff	159.0	1367 *	45.4 *
dw-	*nana Ff*	157.0	1337 *	44.5 *
	Nana Ff	158.5	1357 *	44.8 *

* Significantly different (P<0.05) from the control *nana ff Dw-*

Table 4.10
Probabilities of main and interaction effects on the proportion of onset body weight at 8 and 38 weeks of age

Source of variation	Proportion of onset body weight (%)	
	8 wk	38 wk
Diet (D)	0.104	**<0.001**
Season (S)	**<0.001**	**<0.001**
Na locus	0.135	0.163
F locus	0.516	0.331
dw locus	0.614	**<0.001**
D x S	0.550	0.206
D x *Na*	0.277	0.921
D x *F*	0.160	0.472
D x *dw*	0.130	0.475
S x *Na*	*0.053*	**0.032**
S x *F*	0.287	0.228
S x *dw*	0.270	**0.004**
Na x *F*	0.753	0.485
Na x *dw*	0.228	0.635
F x *dw*	0.216	0.314

Table 4.11
LS-means of main effects on the proportion of onset body weight at 8 and 38 weeks of age

Factor		Proportion of onset body weight (%)	
		8 wk	38 wk
	μ	32.1	111.1
	SE	0.2	0.4
Diet	HP	31.8	112.8
	LP	32.3	109.4
Season	Exp. 1	28.7	107.7
	Exp. 2	35.5	114.5
Na	*Nana*	31.8	111.6
locus	*Nana*	32.3	110.6
F	*Ff*	32.0	110.8
locus	*Ff*	32.2	111.4
dw	*Dw-*	32.2	113.6
locus	*dw-*	32.0	108.6

Table 4.12
LS-means of interaction effects on the proportion of onset body weight at 38-wk of age

Season x *Na* locus			Season x *dw* locus		
	38 wk (μ=111.1)			38 wk (μ=111.1)	
	nana	*Nana*		*Dw-*	*dw-*
Exp.1	108.9	106.4	Exp.1	111.1	104.1
Exp.2	114.2	114.8	Exp.2	115.9	113.1

Table 4.13
LS-means of the proportion of onset body weight at 8 and 38 weeks of age in the genetic groups

Body size type	Feathering type	Proportion of onset body weight (%)	
		8 wk	38 wk
Dw-	***nana ff***	31.9	113.7
	Nana ff	32.6 *	112.0
	nana Ff	31.5	114.1
	Nana Ff	32.6 *	114.5
dw-	*nana ff*	31.6	109.3 *
	Nana ff	31.8	108.0 *
	nana Ff	32.3	109.3 *
	Nana Ff	32.3	107.9 *

* Significantly different (P<0.05) from the control *nana ff Dw-*

Table 4.14
Phenotypic correlations between traits at sexual maturity

Body size type	Exp. 1	Exp. 2
	Age and egg weight	
Dw-	0.38 **	0.40 **
dw-	0.49 **	0.61 **
	Body weight and egg weight	
Dw-	0.09	0.38 **
dw-	0.17 *	0.41 **

* P<0.05; ** P<0.01

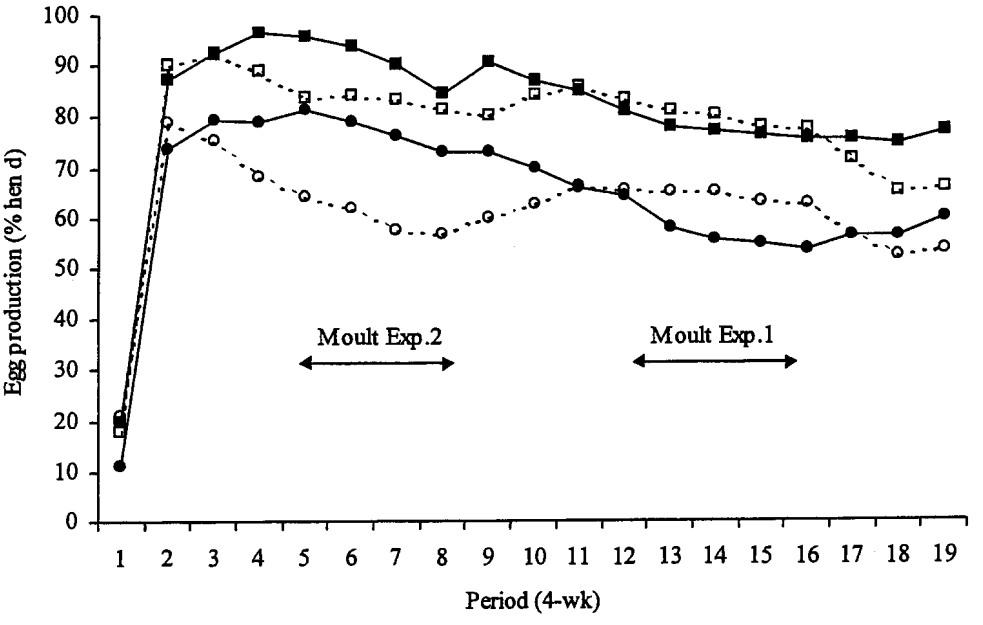


Figure 4.9 - Period and incidence of the natural moult on egg production (% hen d) (normal size: ■—■ Exp. 1, □----□ Exp. 2; dwarf: ●—● Exp. 1, ○----○ Exp. 2).

Table 4.15

Probabilities of main and interaction effects on egg number

Source of variation	Egg number (eggs/hen)				
	LC I				LC II
	1-8 wk	9-30 wk	31-52 wk	1-52 wk	53-76 wk
Diet (D)	0.987	0.190	0.513	0.432	0.625
Season (S)	**0.001**	**<0.001**	**<0.001**	**<0.001**	0.776
Na locus	0.297	0.233	0.132	0.231	0.754
F locus	0.775	0.202	0.420	0.301	**0.023**
dw locus	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
D x S	0.977	0.111	0.270	0.240	0.890
D x *Na*	0.660	**0.024**	0.131	0.066	0.425
D x *F*	0.960	0.895	0.575	0.776	0.364
D x *dw*	0.253	0.217	0.977	0.899	0.359
S x *Na*	**0.017**	0.649	0.824	0.252	0.727
S x *F*	0.574	0.755	0.694	0.592	0.468
S x *dw*	**<0.001**	**0.001**	0.057	0.154	**0.029**
Na x *F*	0.434	0.785	0.149	0.607	**0.016**
Na x *dw*	0.066	0.396	0.436	0.161	0.995
F x *dw*	0.745	0.070	0.836	0.351	0.482

Table 4.16

LS-means of main effects on egg number

Factor		Egg number (eggs/hen)				
		LC I				LC II
		1-8 wk	9-30 wk	31-52 wk	1-52 wk	53-76 wk
	μ	24.6	125.1	114.8	264.1	104.0
	SE	0.4	0.7	0.7	1.3	1.3
Diet	HP	24.6	125.9	115.2	265.1	110.1
	LP	24.7	124.2	114.3	263.0	109.0
Season	Exp. 1	23.1	132.0	117.3	272.3	109.9
	Exp. 2	26.1	118.1	112.3	255.7	109.3
Na	*nana*	25.2	124.3	113.7	262.4	109.2
locus	*Nana*	24.1	125.9	115.8	265.6	109.9
F	*ff*	24.9	125.9	115.3	265.3	111.9
locus	*Ff*	24.4	124.2	114.2	262.7	107.2
dw	*Dw-*	26.6	138.7	128.9	294.1	123.7
locus	*dw-*	22.7	111.4	100.7	234.0	95.4

Table 4.17

LS-means of interaction effects on egg number (eggs/hen)

Season x *dw* locus						
	1-8 wk (μ=24.6)		9-30 wk (μ=125.1)		53-76 wk (μ=109.6)	
	Dw-	*dw-*	*Dw-*	*dw-*	*Dw-*	*dw-*
Exp.1	27.1	19.3	143.5	120.4	126.3	93.4
Exp.2	26.1	26.1	133.8	101.8	121.1	97.4

Diet x *Na* locus		
	9-30 wk (μ=125.1)	
	nana	*Nana*
HP	126.4	125.2
LP	121.6	126.4

Season x *Na* locus		
	1-8 wk (μ=24.6)	
	nana	*Nana*
Exp.1	24.8	21.6
Exp.2	25.6	26.6

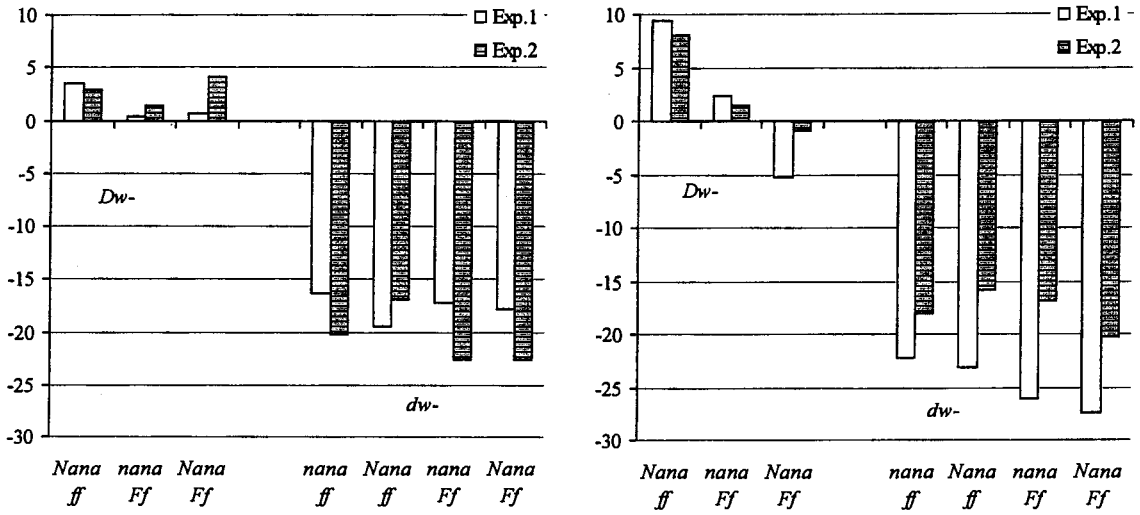
***Na* x *F* locus**		
	53-76 wk (μ=109.6)	
	ff	*Ff*
nana	109.1	109.4
Nana	114.8	105.0

Table 4.18

LS-means of egg number in the genetic groups

Body size type	Feathering type	Egg number (eggs/hen)				
		LC I				LC II
		1-8 wk	9-30 wk	31-52 wk	1-52 wk	53-76 wk
Dw-	***nana ff***	26.6	136.4	126.5	289.4	118.0
	Nana ff	26.4	140.4	132.6	298.9	126.1
	nana Ff	26.2	138.4	128.1	291.6	116.2
	Nana Ff	27.3	139.8	128.2	296.1	110.1
dw-	*nana ff*	25.0	112.7 *	99.8 *	236.5 *	96.8 *
	Nana ff	21.5	113.1 *	102.1 *	236.5 *	97.6 *
	nana Ff	23.1	108.8 *	100.3 *	231.9 *	95.1 *
	Nana Ff	21.2 *	109.9 *	100.3 *	231.0 *	92.2 *

* Significantly different (P<0.05) from the control *nana ff Dw-*



(i) LC I (ii) LC II

Figure 4.10 – Egg number by genetic group and experiment (as % deviation from the normal type)

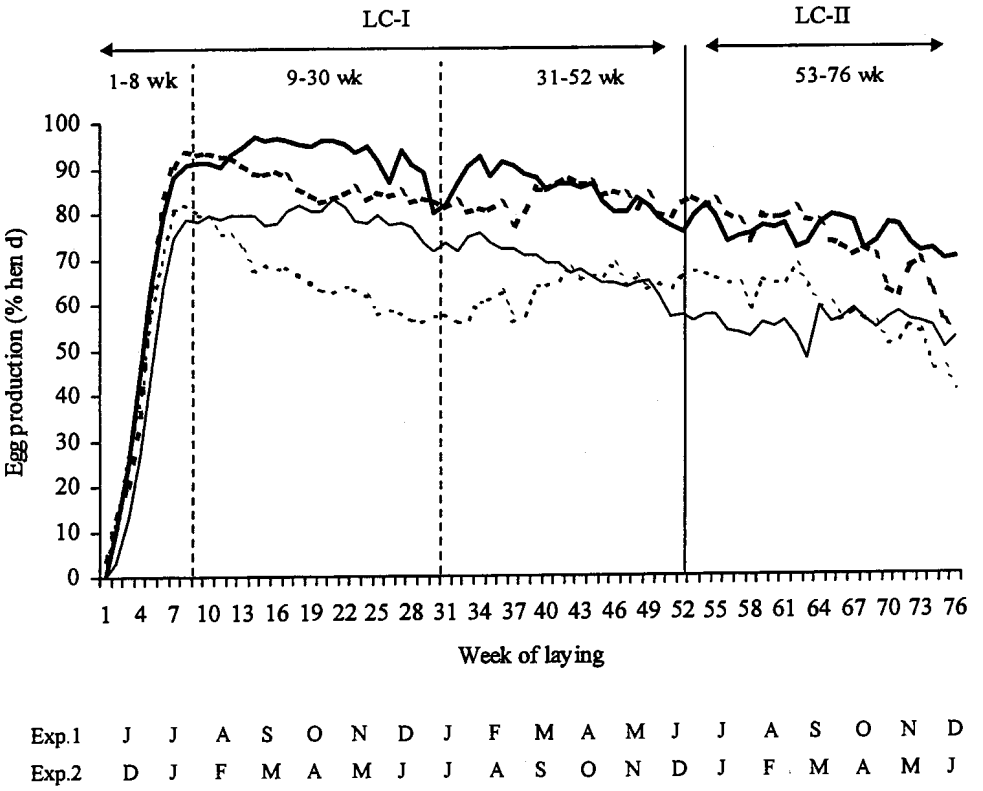


Figure 4.11 - Laying rate by body size group and experiment
(Normal size: —— Exp. 1, – – Exp. 2; Dwarf: ——Exp. 1, --- Exp. 2)

Table 4.19
Averaged laying rate by body size group and experiment

Body size type	Laying rate (%)				
	LC I				LC II
	1-8 wk	9-30 wk	31-52 wk	1-52 wk	53-76 wk
Experiment 1					
Normal	50.2	92.8	84.7	82.8	75.2
Dwarf	38.2	78.6	67.7	67.8	55.0
dw-/Dw-	-12.0	-14.2	-17.0	-15.0	-20.2
Experiment 2					
Normal	50.3	86.6	82.6	79.3	72.4
Dwarf	47.2	65.7	62.7	61.6	58.3
dw-/Dw-	-3.1	-20.9	-19.9	-17.7	-14.1

Table 4.20
Probabilities of main and interaction effects on persistence

Source of variation	LC I P(60%) wk	LC I EN 31-52 wk / EN 9-30 wk	LC II EN 53-76 wk / EN 31-52 wk
Diet (D)	0.616	0.996	0.443
Season (S)	**<0.001**	**<0.001**	**0.003**
Na locus	0.495	0.619	0.674
F locus	0.619	0.460	**0.029**
dw locus	**<0.001**	0.673	0.764
D x S	0.631	0.740	0.910
D x *Na*	0.742	0.905	0.159
D x *F*	0.452	0.903	0.462
D x *dw*	0.929	0.992	0.322
S x *Na*	0.555	0.697	0.731
S x *F*	0.949	0.496	0.211
S x *dw*	**0.001**	**0.010**	**<0.001**
Na x *F*	0.960	0.527	0.105
Na x *dw*	0.802	0.646	0.657
F x *dw*	0.300	0.054	0.759

Table 4.21
LS-means of main effects on persistence

Factor		LC I P (60%) wk	LC I EN 31-52 wk / EN 9-30 wk	LC II EN 53-76 wk / EN 31-52 wk
	μ	28.0	0.93	0.95
	SE	0.1	0.01	0.01
Diet	HP	27.9	0.93	0.94
	LP	28.0	0.93	0.96
Season	Exp. 1	27.6	0.89	0.93
	Exp. 2	28.4	0.97	0.97
Na	*nana*	27.9	0.92	0.95
locus	*Nana*	28.0	0.93	0.95
F	*ff*	28.0	0.92	0.97
locus	*Ff*	27.9	0.93	0.93
dw	*Dw-*	28.4	0.93	0.95
locus	*dw-*	27.5	0.92	0.95

Table 4.22

LS-means of interaction effects on persistence

Season x *dw* locus						
	P(60%) (μ=28.0)		EN 31-52 wk EN 9-30 wk (μ=0.93)		EN 53-76 wk EN 31-52 wk (μ=0.95)	
	Dw-	*dw-*	*Dw-*	*dw-*	*Dw-*	*dw-*
Exp.1	28.4	27.4	0.91	0.86	0.96	0.89
Exp.2	28.5	28.2	0.96	0.98	094	1.01

Table 4.23

LS-means of persistence in the genetic groups

		LC I		LC II
Body size type	Feathering type	P (60%) wk	EN 31-52 wk EN 9-30 wk	EN 53-76 wk EN 31-52 wk
Dw-	***nana ff***	28.5	0.93	0.95
	Nana ff	28.7	0.95	1.00
	nana Ff	28.4	0.93	0.96
	Nana Ff	28.3	0.91	0.91
dw-	*nana ff*	27.4 *	0.90	0.97
	Nana ff	27.5	0.91	0.96
	nana Ff	27.4 *	0.94	0.94
	Nana Ff	27.6	0.95	0.93

* Significantly different (P<0.05) from the control *nana ff Dw-*

Table 4.24

Probabilities of main and interaction effects on egg weight

Source of variation	Egg weight (g)				
	LC I				LC II
	1-8 wk	9-30 wk	31-52 wk	1-52 wk	53-76 wk
Diet (D)	0.403	0.080	0.398	0.194	0.170
Season (S)	**<0.001**	**<0.001**	0.682	**<0.001**	**<0.001**
Na locus	0.857	0.672	0.672	0.453	0.973
F locus	0.551	0.253	0.167	0.225	0.327
dw locus	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
D x S	**0.013**	**0.026**	**0.043**	**0.024**	0.316
D x *Na*	**0.008**	0.164	**0.030**	**0.020**	0.062
D x *F*	0.194	0.936	0.475	0.489	0.085
D x *dw*	0.723	0.463	0.521	0.502	0.507
S x *Na*	0.719	0.149	0.077	0.108	0.299
S x *F*	0.075	0.057	**0.011**	**0.048**	**0.008**
S x *dw*	**0.001**	0.969	**0.020**	0.080	**0.026**
Na x *F*	0.243	0.644	0.502	0.797	0.705
Na x *dw*	0.593	0.142	0.282	0.152	0.835
F x *dw*	0.835	0.549	0.874	0.684	0.831

Table 4.25

LS-means of main effects on egg weight

Factor		Egg weight (g)				
		LC I				LC II
		1-8 wk	9-30 wk	31-52 wk	1-52 wk	53-76 wk
	μ	53.1	59.4	62.8	58.5	64.2
	SE	0.1	0.1	0.2	0.1	0.2
Diet	HP	53.2	59.6	62.9	58.7	64.4
	LP	53.0	59.2	62.6	58.3	64.0
Season	Exp. 1	55.7	60.5	62.9	59.7	65.3
	Exp. 2	50.5	58.3	62.8	57.3	63.0
Na	*nana*	53.0	59.3	62.7	58.4	64.1
locus	*Nana*	53.2	59.5	62.8	58.6	64.2
F	*ff*	53.0	59.2	62.5	58.3	64.0
locus	*Ff*	53.2	59.6	63.0	58.7	64.3
dw	*Dw-*	55.8	62.4	65.1	61.2	66.4
locus	*dw-*	50.4	56.4	60.4	55.8	62.0

Table 4.26

LS-means of interaction effects on egg weight

Diet x Season								
	1-8 wk (μ=53.1)		9-30 wk (μ=59.4)		31-52 wk (μ=62.8)		1-52 wk (μ=58.5)	
	Exp.1	Exp.2	Exp.1	Exp.2	Exp.1	Exp.2	Exp.1	Exp.2
HP	55.5	50.9	60.4	60.0	62.5	63.4	59.6	57.9
LP	55.9	50.1	60.5	57.9	62.9	62.3	59.8	56.8

Diet x *Na* locus						
	1-8 wk (μ=53.1)		31-52 wk (μ=62.8)		1-52 wk (μ=58.5)	
	nana	*Nana*	*nana*	*Nana*	*nana*	*Nana*
HP	53.5	52.9	63.2	62.6	58.9	58.5
LP	52.6	53.4	62.2	63.0	57.9	58.7

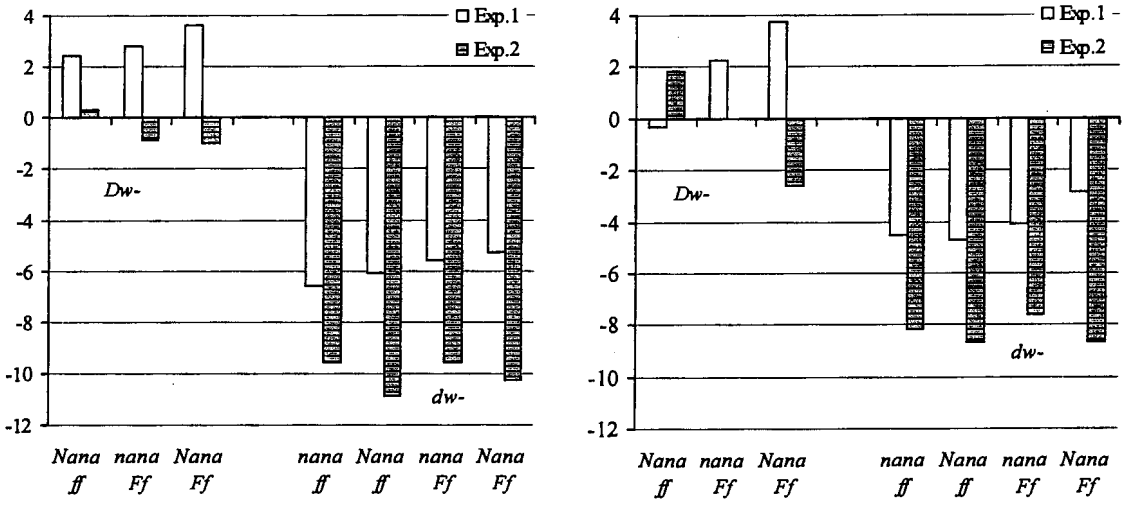
Season x *F* locus						
	31-52 wk (μ=62.8)		1-52 wk (μ=58.5)		53-76 wk (μ=64.2)	
	ff	*Ff*	*ff*	*Ff*	*ff*	*Ff*
Exp.1	62.0	63.3	59.2	60.1	64.6	66.0
Exp.2	63.0	62.6	57.5	57.2	63.4	62.6

Season x *dw* locus						
	1-8 wk (μ=53.1)		31-52 wk (μ=62.8)		53-76 wk (μ=64.2)	
	Dw-	*dw-*	*Dw-*	*dw-*	*Dw-*	*dw-*
Exp.1	58.0	53.4	64.7	60.7	67.2	63.5
Exp.2	53.7	47.3	65.6	60.0	65.8	60.4

Table 4.27
LS-means of egg weight in the genetic groups

Body size type	Feathering type	Egg weight (g)				
		LC I				LC II
		1-8 wk	9-30 wk	31-52 wk	1-52 wk	53-76 wk
Dw-	***nana ff***	55.6	62.1	64.7	60.7	66.2
	Nana ff	56.0	62.5	65.2	61.5	66.6
	nana Ff	55.8	62.1	65.1	61.1	66.8
	Nana Ff	55.9	62.8	65.6	61.5	66.8
dw-	*nana ff*	50.0 *	56.4 *	60.4 *	55.7 *	61.8 *
	Nana ff	50.5 *	56.0 *	59.8 *	55.4 *	61.7 *
	nana Ff	50.7 *	56.7 *	60.5 *	56.0 *	62.2 *
	Nana Ff	50.2 *	56.6 *	60.7 *	55.9 *	62.2 *

* Significantly different (P<0.05) from the control *nana ff Dw-*



(i) LC I (ii) LC II

Figure 4.12 – Egg weight by genetic group and experiment (as % deviation from normal type)

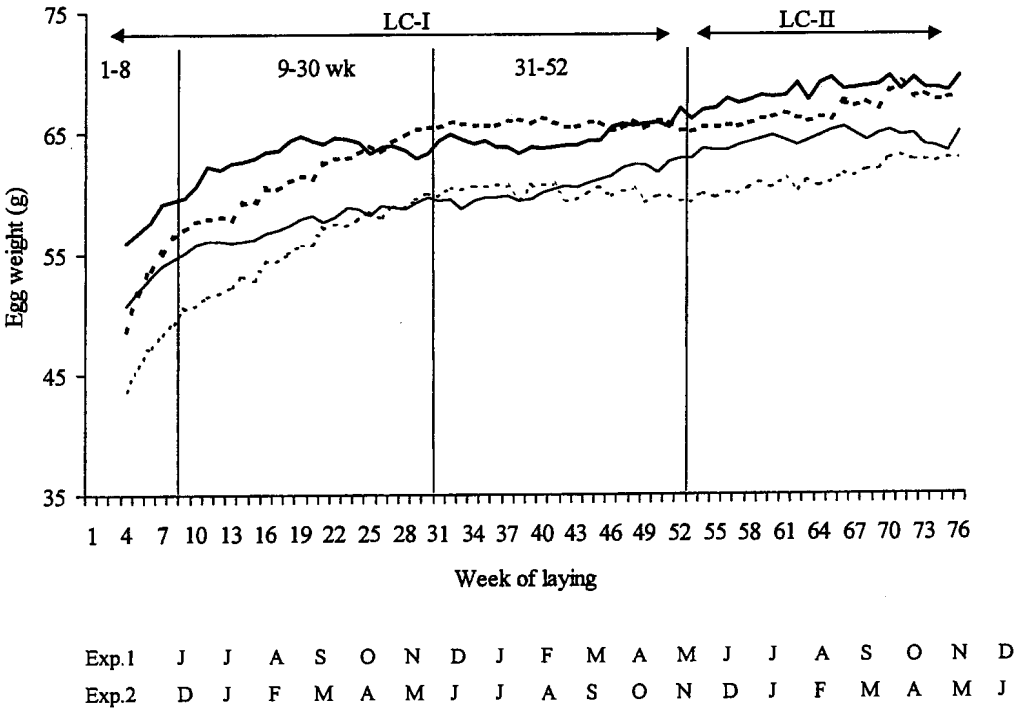


Fig. 4.13 – Egg weight curves by body size group and experiment
(Normal size: —— Exp. 1, - - Exp. 2; Dwarf: ——Exp. 1, ---Exp. 2)

Table 4.28

Parameter estimates of the equation $Y=A-Br^t$ for combined egg weight by body size group within experiment in the first laying cycle

Body size type	Parameter				
	A	*B*	*r*	R^2	RSD [1]
Experiment 1					
Normal	64.6	16.8	0.86	0.89	0.75
Dwarf	63.1	12.5	0.96	0.94	0.64
Experiment 2					
Normal	66.3	22.3	0.92	0.98	0.66
Dwarf	60.9	23.7	0.92	0.98	0.66

[1] RSD = Residual standard deviation from the equation

Table 4.29

Probabilities of main and interaction effects on egg mass

Source of variation	Egg mass (kg/hen)				
	LC I				LC II
	1-8 wk	9-30 wk	31-52 wk	1-52 wk	53-76 wk
Diet (D)	0.735	0.082	0.229	0.226	0.540
Season (S)	0.906	**<0.001**	**0.002**	**<0.001**	**0.048**
Na locus	0.293	0.112	0.071	0.243	0.473
F locus	0.759	0.690	0.953	0.540	**0.037**
dw locus	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
D x S	0.672	0.338	0.817	0.513	0.896
D x *Na*	0.475	**0.008**	**0.025**	**0.003**	0.726
D x *F*	0.777	0.697	0.466	0.421	0.680
D x *dw*	0.279	0.641	0.673	0.891	0.337
S x *Na*	**0.011**	0.783	0.336	0.791	0.927
S x *F*	0.629	0.170	0.186	0.053	0.579
S x *dw*	**<0.001**	**0.011**	**0.004**	0.158	0.070
Na x *F*	0.444	0.699	0.157	0.337	**0.013**
Na x *dw*	0.080	**0.042**	0.183	0.075	0.183
F x *dw*	0.820	0.178	0.766	0.742	0.456

Table 4.30

LS-means of main effects on egg mass

Factor		Egg mass (kg/hen)				
		LC I				LC II
		1-8 wk	9-30 wk	31-52 wk	1-52 wk	53-76 wk
	μ	1.30	7.48	7.23	15.96	7.13
	SE	0.02	0.04	0.04	0.08	0.07
Diet	HP	1.31	7.54	7.28	16.06	7.17
	LP	1.29	7.41	7.18	15.86	7.09
Season	Exp. 1	1.31	8.02	7.37	16.66	7.26
	Exp. 2	1.30	6.94	7.10	15.27	7.00
Na	*nana*	1.33	7.42	7.15	15.86	7.08
locus	*Nana*	1.28	7.54	7.31	16.06	7.18
F	*ff*	1.31	7.49	7.23	16.01	7.27
locus	*Ff*	1.30	7.46	7.23	15.91	6.99
dw	*Dw-*	1.48	8.65	8.39	18.46	8.31
locus	*dw-*	1.12	6.31	6.07	13.46	5.95

Table 4.31

LS-means of interaction effects on egg mass (kg/hen)

Season x *dw* locus

	1-8 wk (μ=1.30)		9-30 wk (μ=7.48)		31-52 wk (μ=7.23)	
	Dw-	*dw-*	*Dw-*	*dw-*	*Dw-*	*dw-*
Exp.1	1.57	1.03	9.09	6.94	8.40	6.33
Exp.2	1.39	1.21	8.20	5.67	8.38	5.83

Diet x *Na* locus

	9-30 wk (μ=7.48)		31-52 wk (μ=7.23)		1-52 wk (μ=15.96)	
	nana	*Nana*	*nana*	*Nana*	*nana*	*Nana*
HP	7.58	7.50	7.30	7.26	16.21	15.91
LP	7.25	7.57	7.01	7.35	15.92	16.20

Season x *Na* locus

	1-8 wk (μ=1.30)	
	Exp.1	Exp.2
nana	1.39	1.27
Nana	1.22	1.33

***Na* x *F* locus**

	53-76 wk (μ=7.13)	
	nana	*Nana*
ff	7.06	7.48
Ff	7.11	6.87

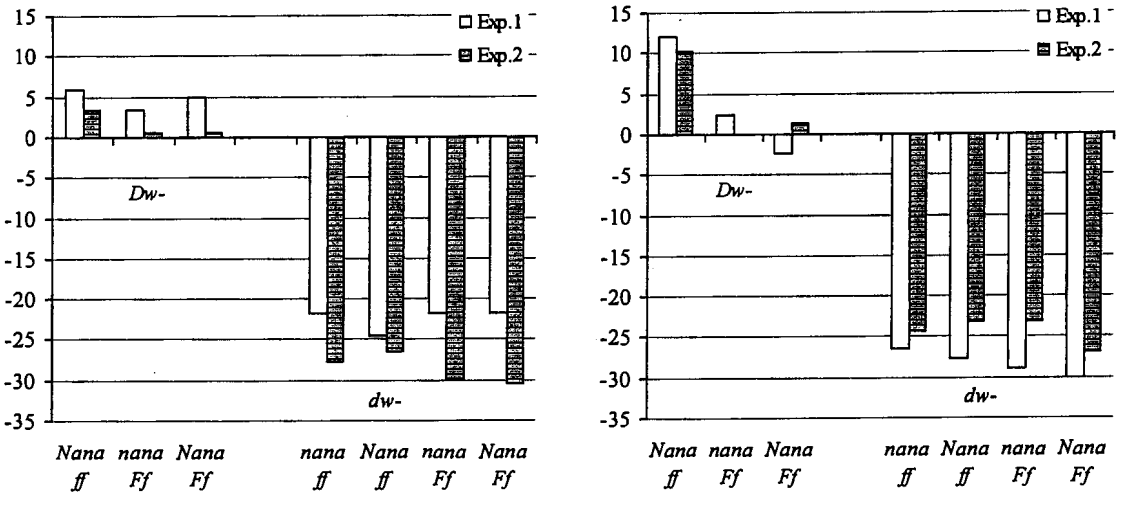
***Na* x *dw* locus**

	9-30 wk (μ=7.48)	
	nana	*Nana*
Dw	8.51	8.78
dw	6.32	6.29

Table 4.32
LS-means of egg mass in the genetic groups

Body size type	Feathering type	Egg mass (kg/hen)				
		LC I				LC II
		1-8 wk	9-30 wk	31-52 wk	1-52 wk	53-76 wk
Dw-	***nana ff***	1.49	8.43	8.16	18.07	8.09
	Nana ff	1.48	8.79	8.65 *	18.89	8.91 *
	nana Ff	1.44	8.59	8.35	18.36	8.26
	Nana Ff	1.52	8.78	8.40	18.51	7.99
dw-	*nana ff*	1.21 *	6.40 *	6.03 *	13.60 *	6.02 *
	Nana ff	1.06 *	6.35 *	6.10 *	13.47 *	6.06 *
	nana Ff	1.16 *	6.25 *	6.08 *	13.42 *	5.96 *
	Nana Ff	1.06 *	6.23 *	6.09 *	13.35 *	5.76 *

* Significantly different (P<0.05) from the control *nana ff Dw-*



(i) LC I (ii) LC II

Figure 4.14 – Egg mass by genetic group and experiment (as % deviation from normal type)

Table 4.33
Probabilities of main and interaction effects
on biological efficiency (EMD/BW$^{0.75}$) and productivity (EN/BW$^{0.75}$)

Source of variation	Biological efficiency (g:kg$^{0.75}$)		Productivity (eggs:kg$^{0.75}$)	
	LC I	LC II	LC I	LC II
	1-52 wk	53-76 wk	1-52 wk	53-76 wk
Diet (D)	0.850	0.751	0.747	0.685
Season (S)	**<0.001**	0.382	0.056	**0.010**
Na locus	**0.024**	0.172	**0.036**	0.309
F locus	0.677	0.222	0.945	0.149
dw locus	0.914	0.132	**<0.001**	**0.009**
D x S	0.767	0.907	0.311	0.753
D x *Na*	**0.004**	0.441	0.140	0.221
D x *F*	0.475	0.410	0.939	0.229
D x *dw*	0.971	0.659	0.888	0.610
S x *Na*	0.324	0.553	0.787	0.864
S x *F*	0.097	0.759	0.695	0.629
S x *dw*	**<0.001**	0.465	**0.001**	0.167
Na x *F*	0.094	**0.009**	0.231	**0.016**
Na x *dw*	0.372	0.387	0.708	0.740
F x *dw*	0.781	0.308	0.786	0.451

Table 4.34
LS-means of main effects
on biological efficiency (EMD/BW$^{0.75}$) and productivity (EN/BW$^{0.75}$)

Factor		Biological efficiency (g:kg$^{0.75}$)		Productivity (eggs:kg$^{0.75}$)	
		LC I	LC II	LC I	LC II
		1-52 wk	53-76 wk	1-52 wk	53-76 wk
	μ	28.2	25.9	171.3	67.4
	SE	0.1	0.4	1.0	0.6
Diet	HP	28.2	25.9	171.0	67.2
	LP	28.2	26.0	171.6	67.7
Season	Exp. 1	28.9	25.7	173.2	65.7
	Exp. 2	27.5	26.1	169.4	69.1
Na	*nana*	27.9	25.6	169.2	66.8
locus	*Nana*	28.5	26.3	173.4	68.1
F	*ff*	28.1	26.2	171.4	68.4
locus	*Ff*	28.3	25.7	171.3	66.5
dw	*Dw-*	28.2	26.3	163.9	65.7
locus	*dw-*	28.2	25.6	178.8	69.1

Table 4.35
LS-means of interaction effects on biological efficiency ($EMD/BW^{0.75}$) and productivity ($EN/BW^{0.75}$)

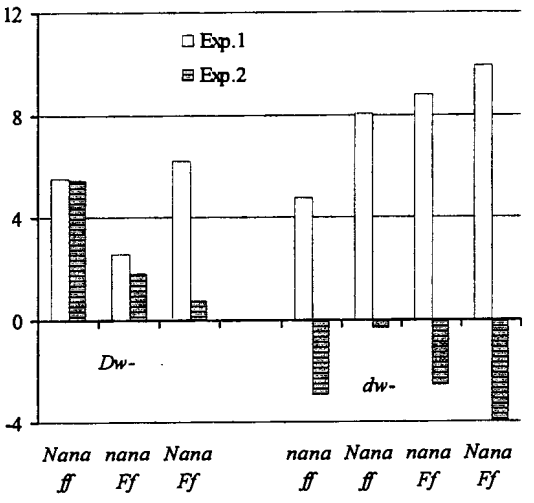
Season x *dw* locus (1-52 wk)				
	$EM/BW^{0.75}$ (μ=10.3)		$EN/BW^{0.75}$ (μ=171.3)	
	Dw-	*dw-*	*Dw-*	*dw-*
Exp.1	28.3	29.5	162.6	183.8
Exp.2	28.1	26.9	165.1	173.7

***Na* x *F* locus (53-76 wk)**				
	$EM/BW^{0.75}$ (μ=4.36)		$EN/BW^{0.75}$ (μ=67.4)	
	nana	*Nana*	*ff*	*Ff*
ff	25.3	27.1	66.1	67.4
Ff	25.9	25.4	70.6	65.6

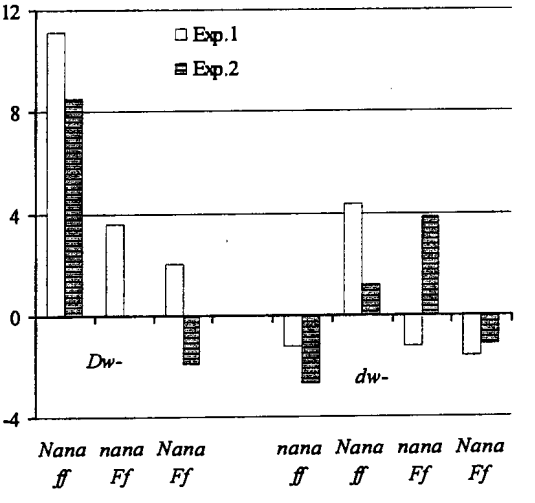
D x *Na* locus (1-52 wk)		
	$EM/BW^{0.75}$ (μ=10.3)	
	nana	*Nana*
HP	28.3	28.1
LP	27.4	28.9

Table 4.36
LS-means of biological efficiency ($EMD/BW^{0.75}$) and productivity ($EN/BW^{0.75}$) in the genetic groups

Body size type	Feathering type	Biological efficiency ($g:kg^{0.75}$)		Productivity ($eggs:kg^{0.75}$)	
		LC I	LC II	LC I	LC II
		1-52 wk	53-76 wk	1-52 wk	53-76 wk
Dw-	***nana ff***	27.5	25.6	160.4	64.4
	Nana ff	29.0	28.1 *	167.0	70.0
	nana Ff	28.1	26.0	162.4	65.4
	Nana Ff	28.4	25.6	165.6	63.2
dw-	*nana ff*	27.7	25.1	175.9 *	67.9
	Nana ff	28.5	26.2	182.3 *	71.2 *
	nana Ff	28.3	25.9	178.2 *	69.4
	Nana Ff	28.3	28.3	178.6 *	67.9

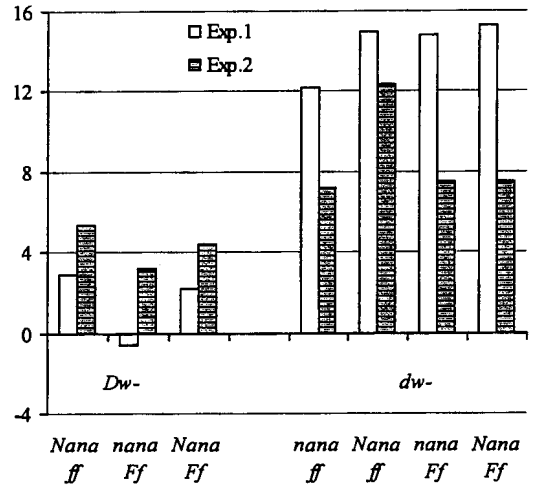


(i) LC I

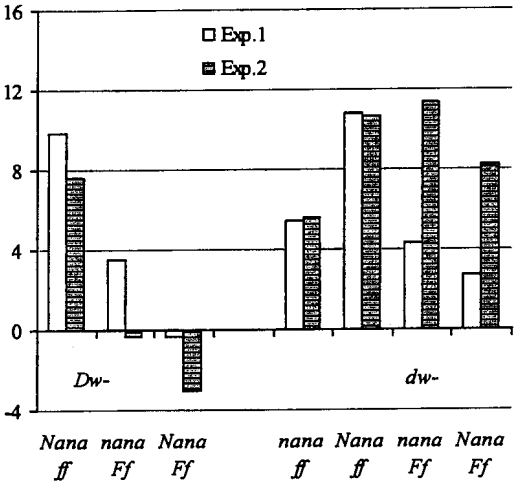


(ii) LC II

(A) Biological efficiency ($EMD/BW^{0.75}$)



(i) LC I



(ii) LC II

(B) Productivity ($EN/BW^{0.75}$)

Figure 4.15 – Biological efficiency and productivity by genetic group and experiment (as % deviation from the normal type)

Table 4.37

Probabilities of main and interaction effects on feed intake per kg $^{0.75}$

Source of variation	Feed intake/kg $^{0.75}$ (g d^{-1})				
	LC I				LC II
	1-8 wk	9-30 wk	31-52 wk	1-52 wk	53-76 wk
Diet (D)	0.114	0.352	0.085	0.163	**<0.001**
Season (S)	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.171
Na locus	**0.038**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
F locus	0.254	**0.002**	**<0.001**	**<0.001**	**<0.001**
dw locus	**<0.001**	**0.022**	0.137	**<0.001**	**0.008**
D x S	0.613	**0.012**	0.180	0.508	0.995
D x *Na*	0.185	0.090	0.177	0.074	0.429
D x *F*	0.065	0.288	0.508	0.280	0.833
D x *dw*	0.658	0.104	0.960	0.555	0.518
S x *Na*	0.974	**0.031**	0.758	0.153	0.320
S x *F*	0.318	0.742	0.184	0.712	0.518
S x *dw*	**0.012**	**<0.001**	**<0.001**	**<0.001**	0.067
Na x *F*	0.070	0.829	0.265	0.590	0.374
Na x *dw*	0.832	0.146	0.597	0.273	0.591
F x *dw*	0.301	0.149	0.175	0.254	0.335

Table 4.38

LS-means of main effects on feed intake per kg $^{0.75}$

Factor		Feed intake/kg $^{0.75}$ (g d^{-1})				
		LC I				LC II
		1-8 wk	9-30 wk	31-52 wk	1-52 wk	53-76 wk
	μ	65.4	67.1	65.6	67.0	64.1
	SE	0.2	0.2	0.2	0.2	0.3
Diet	HP	65.0	66.9	65.2	66.7	62.8
	LP	65.8	67.3	66.0	67.2	65.4
Season	Exp. 1	68.7	69.2	64.8	67.8	64.8
	Exp. 2	62.1	65.0	66.5	66.1	63.8
Na locus	*nana*	64.9	65.6	64.3	65.6	62.7
	Nana	65.9	68.7	67.0	68.3	65.6
F locus	*ff*	65.1	66.5	64.3	66.0	62.3
	Ff	65.7	67.8	66.9	67.9	65.9
dw locus	*Dw-*	67.6	67.6	66.0	67.7	64.8
	dw-	63.2	66.6	65.3	66.2	63.4

Table 4.39

LS-means of interaction effects on feed intake (g d^{-1}) per kg $^{0.75}$

Season x *dw* locus								
	1-8 wk (μ=65.4)		9-30 wk (μ=67.1)		31-52 wk (μ=65.6)		1-52 wk (μ=67.0)	
	Dw-	*dw-*	*Dw-*	*dw-*	*Dw-*	*dw-*	*Dw-*	*dw-*
Exp.1	70.3	67.1	68.4	70.1	64.1	65.5	67.4	68.1
Exp.2	64.8	59.3	66.9	63.2	67.9	65.1	67.9	64.3

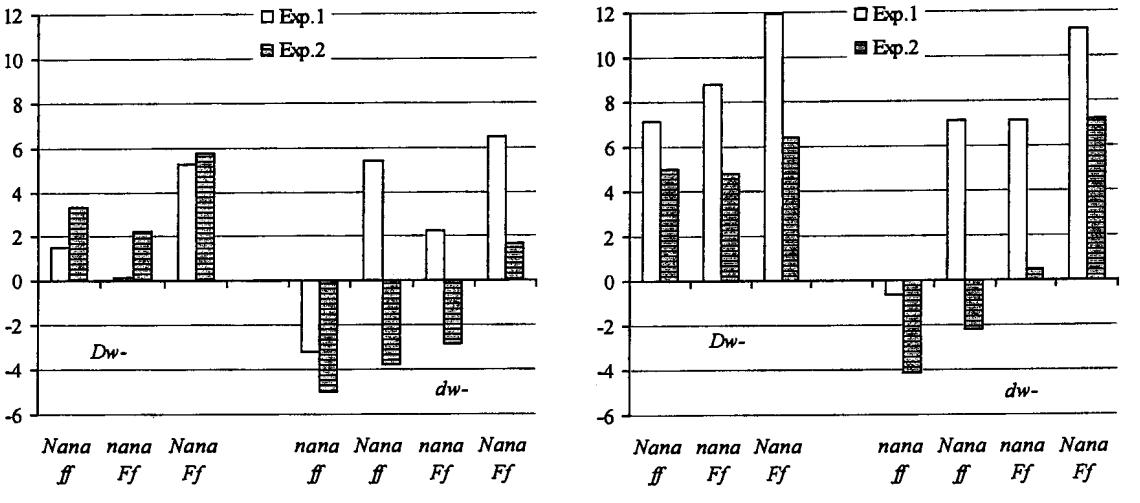
Diet x Season		
	9-30 wk (μ=67.1)	
	HP	LP
Exp.1	68.5	70.0
Exp.2	65.4	64.7

Season x *Na* locus		
	9-30 wk (μ=67.1)	
	nana	*Nana*
Exp.1	67.2	71.2
Exp.2	64.0	66.1

Table 4.40
LS-means of feed intake per kg $^{0.75}$ in the genetic groups

Body size type	Feathering type	Feed intake/kg $^{0.75}$ (g d^{-1})				
		LC I				LC II
		1-8 wk	9-30 wk	31-52 wk	1-52 wk	53-76 wk
Dw-	***nana ff***	67.1	66.6	64.2	66.2	61.4
	Nana ff	67.1	68.0	65.9 *	67.7	65.1 *
	nana Ff	67.2	66.3	65.4	67.0	65.6 *
	Nana Ff	68.9	69.7 *	68.5 *	69.8 *	67.0 *
dw-	*nana ff*	63.1 *	63.2 *	62.4	63.5 *	60.0
	Nana ff	63.3 *	68.1	64.9	66.7	62.9
	nana Ff	62.3 *	66.4	65.3	66.0	63.8 *
	Nana Ff	64.2 *	68.9	68.5 *	68.8 *	67.1 *

* Significantly different (P<0.05) from the control *nana ff Dw-*



(i) LC I (ii) LC II

Figure 4.16 – Feed intake per kg $^{0.75}$ by genetic group and experiment (as % deviation from the normal genotype)

Table 4.41

Probabilities of main and interaction effects on feed efficiency (FI/EM)

Source of variation	Feed efficiency (kg:kg)				
	LC I				LC II
	1-8 wk	9-30 wk	31-52 wk	1-52 wk	53-76 wk
Diet (D)	0.262	0.548	0.448	0.937	0.173
Season (S)	**<0.001**	**<0.001**	**<0.001**	**0.001**	0.813
Na locus	**0.007**	0.228	0.905	0.074	0.777
F locus	0.869	0.064	0.054	**0.005**	**0.002**
dw locus	0.305	0.647	0.480	0.056	0.966
D x S	0.794	0.118	0.253	0.348	0.679
D x *Na*	0.988	0.183	0.133	**0.024**	0.172
D x *F*	0.983	0.895	0.877	0.503	0.504
D x *dw*	0.488	0.741	0.337	0.644	0.894
S x *Na*	**0.007**	0.851	0.393	0.356	0.714
S x *F*	0.486	0.097	0.370	**0.017**	0.830
S x *dw*	**0.017**	**0.001**	0.141	0.341	0.069
Na x *F*	0.649	0.187	**0.005**	**0.008**	**0.036**
Na x *dw*	0.249	**0.041**	0.246	0.184	0.389
F x *dw*	0.616	0.066	0.978	0.970	0.661

Table 4.42

Least square means of main effects on feed efficiency (FI/EM)

Factor		Feed efficiency (kg:kg)				
		LC I				LC II
		1-8 wk	9-30 wk	31-52 wk	1-52 wk	53-76 wk
	μ	5.23	2.22	2.28	2.36	2.57
	SE	0.22	0.02	0.01	0.01	0.03
Diet	HP	4.98	2.21	2.26	2.36	2.52
	LP	5.48	2.23	2.28	2.36	2.62
Season	Exp. 1	6.38	2.15	2.22	2.32	2.58
	Exp. 2	4.08	2.29	2.32	2.40	2.56
Na	*nana*	4.63	2.20	2.27	2.34	2.56
locus	*Nana*	5.83	2.24	2.27	2.38	2.58
F	*ff*	5.19	2.19	2.25	2.32	2.46
locus	*Ff*	5.27	2.25	2.30	2.40	2.68
dw	*Dw-*	5.00	2.21	2.28	2.38	2.57
locus	*dw-*	5.46	2.23	2.26	2.34	2.57

Table 4.43

LS-means of interaction effects on feed efficiency (FI/EM)

Diet x *Na* locus

	1-52 wk (μ=2.36)	
	nana	*Nana*
HP	2.31	2.41
LP	2.36	2.31

Season x *dw* locus

	1-8 wk (μ=5.23)		9-30 wk (μ=2.22)	
	Dw-	*dw-*	*Dw-*	*dw-*
Exp.1	5.19	6.00	2.19	2.11
Exp.2	4.35	3.59	2.23	2.35

Season x *Na* locus

	1-8 wk (μ=5.23)	
	nana	*Nana*
Exp.1	4.94	6.26
Exp.2	3.88	4.06

Season x *F* locus

	1-52 wk (μ=2.36)	
	ff	*Ff*
Exp.1	2.31	2.32
Exp.2	2.33	2.46

***Na* x *dw* locus**

	9-30 wk (μ=2.22)	
	nana	*Nana*
Dw-	2.22	2.20
dw-	2.18	2.27

***Na* x *F* locus**

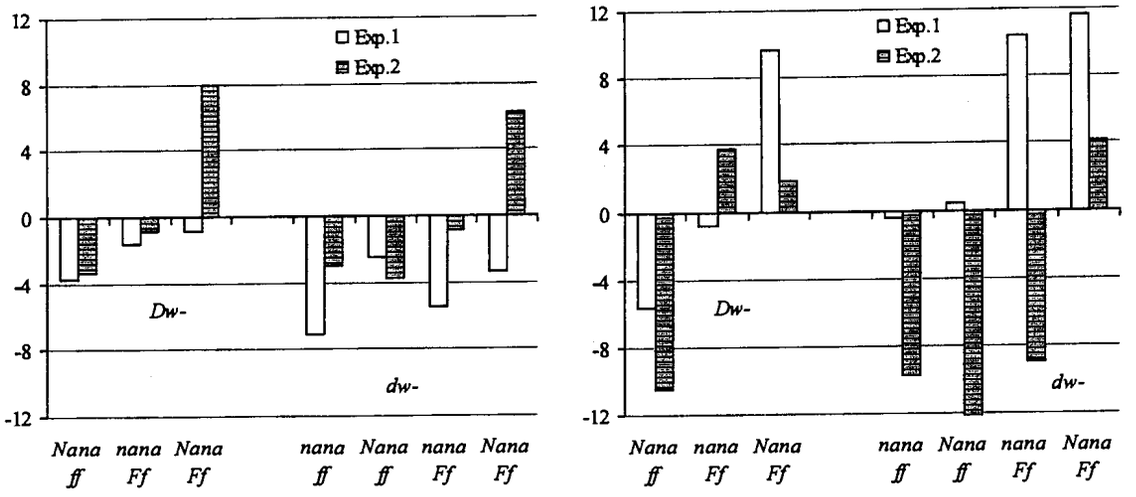
	31-52 wk (μ=2.57)		1-52 wk (μ=2.36)		53-76 wk (μ=2.57)	
	nana	*Nana*	*nana*	*Nana*	*nana*	*Nana*
ff	2.29	2.20	2.33	2.31	2.58	2.45
Ff	2.26	2.34	2.34	2.45	2.65	2.81

Table 4.44

LS-means of feed efficiency (FI/EM) in the genetic groups

Body size type	Feathering type	Feed efficiency (kg:kg)				
		LC I				LC II
		1-8 wk	9-30 wk	31-52 wk	1-52 wk	53-76 wk
Dw-	***nana ff***	4.64	2.26	2.32	2.39	2.59
	Nana ff	5.51	2.17	2.19	2.30	2.37
	nana Ff	4.68	2.20	2.28	2.36	2.60
	Nana Ff	5.18	2.23	2.34	2.47	2.73
dw-	*nana ff*	4.75	2.13	2.25	2.28	2.47
	Nana ff	5.87	2.21	2.22	2.32	2.43
	nana Ff	4.46	2.23	2.24	2.32	2.60
	Nana Ff	6.75	2.34	2.34	2.43	2.79

* Significantly different (P<0.05) from the control *nana ff Dw-*



(i) LC I (ii) LC II

Figure 4.17 – Feed efficiency by genetic group and experiment (as % deviation from the normal genotype)

Table 4.45

Probabilities of main and interaction effects on body weight gain

Source of variation	Body weight gain (g)				
	LC I				LC II
	1-8 wk	9-30 wk	31-52 wk	1-52 wk	53-76 wk
Diet (D)	0.341	*0.053*	**0.012**	**0.001**	0.506
Season (S)	**<0.001**	**<0.001**	0.681	**0.007**	**<0.001**
Na locus	0.571	0.239	0.361	**0.023**	**0.019**
F locus	0.125	0.382	**0.021**	0.225	**0.002**
dw locus	**<0.001**	**<0.001**	0.232	**<0.001**	**0.047**
D x S	0.524	0.280	**0.025**	0.283	0.111
D x *Na*	0.333	0.848	0.274	0.492	0.094
D x *F*	0.394	0.721	0.469	0.374	0.165
D x *dw*	0.178	0.141	0.355	0.981	0.665
S x *Na*	0.284	0.057	**0.014**	0.943	**0.002**
S x *F*	0.437	0.602	0.864	0.242	0.636
S x *dw*	0.820	**0.027**	**0.001**	0.849	0.633
Na x *F*	0.344	0.707	**0.042**	0.734	0.509
Na x *dw*	0.173	0.566	0.713	0.131	0.638
F x *dw*	0.559	0.514	0.202	0.607	**0.011**

Table 4.46

LS-means of main effects on body weight gain

Factor		Body weight gain (g)				
		LC I				LC II
		1-8 wk	9-30 wk	31-52 wk	1-52 wk	53-76 wk
	μ	363.9	140.7	18.4	521.1	36.6
	SE	5.9	5.5	4.6	8.3	5.9
Diet	HP	369.5	151.3	30.0	549.4	32.7
	LP	358.4	130.2	6.8	492.9	40.5
Season	Exp. 1	417.0	69.8	20.3	498.7	11.8
	Exp. 2	310.9	211.7	16.5	543.6	61.3
Na	*nana*	367.3	147.2	22.6	540.0	50.4
locus	*Nana*	360.6	134.3	14.2	502.3	22.7
F	*ff*	372.9	136.0	29.1	531.2	54.6
locus	*Ff*	354.9	145.5	7.8	511.1	18.5
dw	*Dw-*	438.0	185.2	23.9	644.5	24.8
locus	*dw-*	289.9	96.3	12.9	397.8	48.3

Table 4.47

LS-means of interaction effects on body weight gain (g)

Diet x Season		
	31-52 wk (μ=18.4)	
	HP	LP
Exp.1	42.2	-1.8
Exp.2	17.9	15.2

Season x *dw* locus				
	9-30 wk (μ=140.7)		31-52 wk (μ=18.4)	
	Dw-	*dw-*	*Dw-*	*dw-*
Exp.1	126.3	13.2	10.6	30.0
Exp.2	244.0	179.3	37.3	- 4.2

Season x *Na* locus				
	31-52 wk (μ=18.4)		53-76 wk (μ=37.1)	
	nana	*Nana*	*nana*	*Nana*
Exp.1	35.8	4.8	11.5	12.2
Exp.2	9.4	23.6	90.6	34.2

***Na* x *F* locus**		
	31-52 wk (μ=18.4)	
	nana	*Nana*
ff	42.6	15.5
Ff	2.6	12.9

***F* x *dw* locus**		
	53-76 wk (μ=37.1)	
	Dw-	*dw-*
ff	57.9	53.3
Ff	-8.1	45.3

Table 4.48

LS-means of body weight gain in the genetic groups

Body size type	Feathering type	Body weight gain (g)				
		LC I				LC II
		1-8 wk	9-30 wk	31-52 wk	1-52 wk	53-76 wk
Dw-	***nana ff***	436.7	186.4	63.5	676.2	80.4
	Nana ff	450.5	167.3	17.4 *	624.3	35.4
	nana Ff	461.9	203.1	- 3.8 *	675.4	2.5 *
	Nana Ff	402.9	183.9	18.6 *	601.9	- 19.0 *
dw-	*nana ff*	304.7 *	94.3 *	21.8 *	429.5 *	64.3
	Nana ff	299.9 *	95.9 *	13.6 *	394.9 *	38.4
	nana Ff	265.7 *	104.9 *	9.1 *	378.8 *	54.5
	Nana Ff	289.2 *	90.1 *	7.2 *	388.2 *	36.1

* Significantly different (P<0.05) from the control *nana ff Dw-*

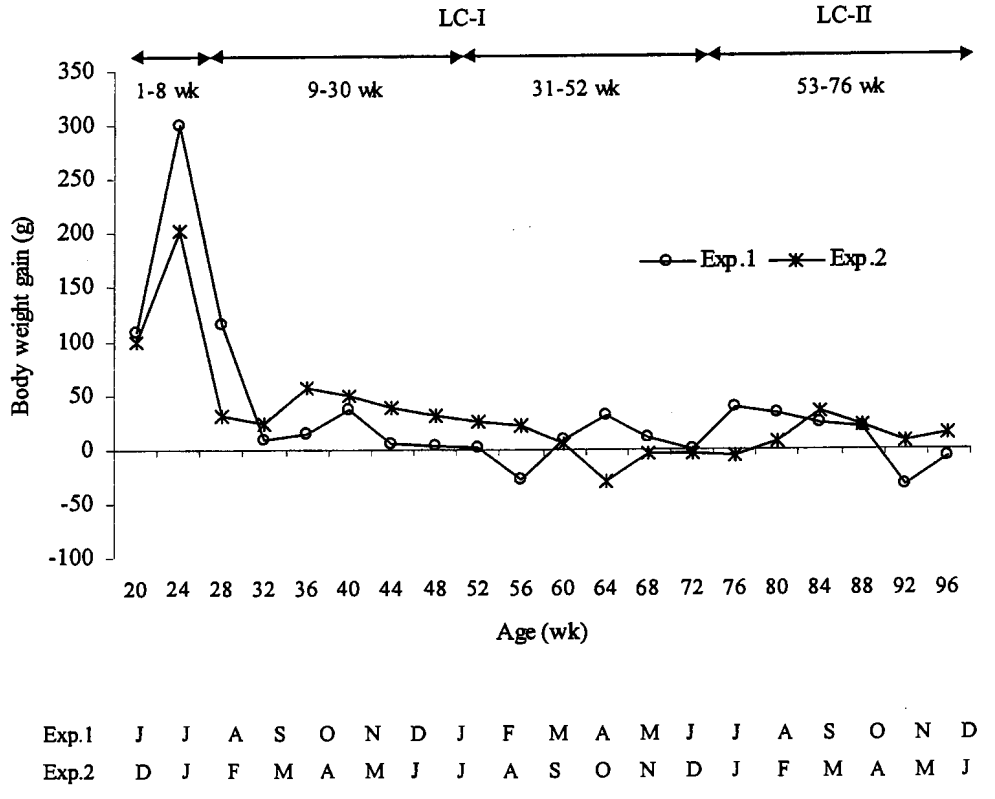


Figure 4.18 - Time trend of body weight gain of layers
(data from normal and dwarf groups was pooled)

Table 4.49
Probabilities of main and interaction effects on the liveability of laying hens

Source of variation	Liveability (%) LC I 1-52 wk	LC II [1] 53-76 wk
Diet (D)	0.634	0.746
Season (S)	**<0.001**	0.355
Na locus	0.651	**0.042**
F locus	0.787	0.969
dw locus	**0.027**	0.310
D x S	0.227	0.951
D x *Na*	0.203	0.069
D x *F*	0.076	0.769
D x *dw*	0.754	0.707
S x *Na*	0.215	0.412
S x *F*	0.289	0.370
S x *dw*	**0.020**	0.612
Na x *F*	0.951	0.875
Na x *dw*	0.209	0.608
F x *dw*	0.475	0.342

[1] Calculated over the birds commencing LC II

Table 4.50
LS-means of main effects on liveability of laying hens

Factor		Liveability (%) LC I	LC II
	μ	91.8	95.8
	SE	1.1	0.8
Diet	HP	92.3	95.5
	LP	91.3	96.0
Season	Exp. 1	86.5	96.5
	Exp. 2	97.2	95.0
Na locus	*nana*	92.3	94.0
	Nana	91.3	97.5
F locus	*ff*	91.5	95.8
	Ff	92.1	95.7
dw locus	*Dw*	89.4	94.9
	dw	94.3	96.6

Table 4.51
LS-means for liveability of genetic groups adjusted for main effects

Body size type	Feathering type	Liveability (%) LC I 1-52 wk	LC II 53-76 wk
Dw-	***nana ff***	89.0	93.6
	Nana ff	87.7	97.9
	nana Ff	93.5	91.9
	Nana Ff	87.4	96.2
dw-	*nana ff*	95.2	94.8
	Nana ff	94.3	96.8
	nana Ff	91.5	95.8
	Nana Ff	96.0	99.0

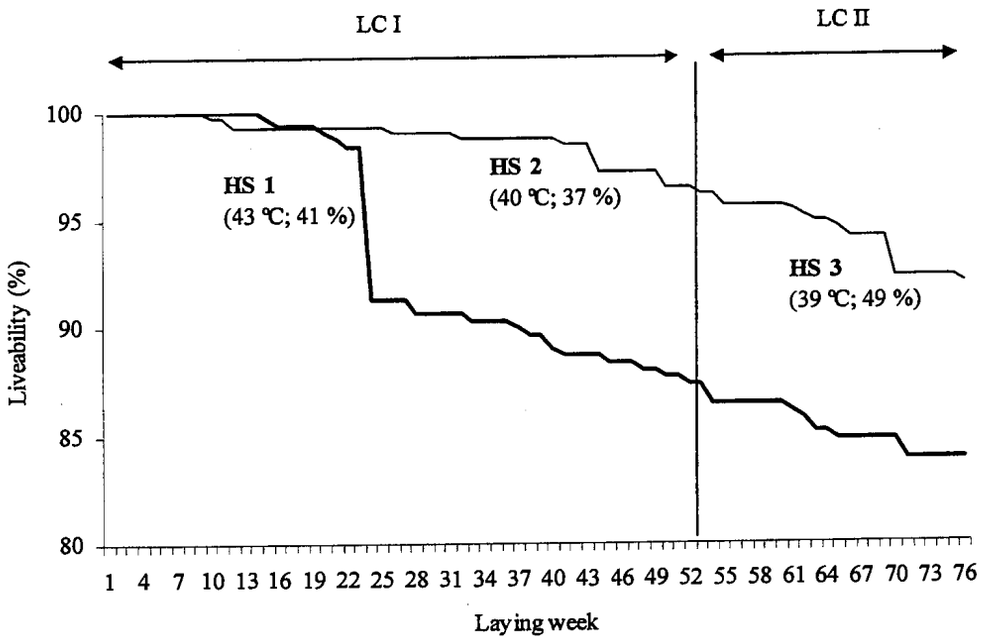


Figure 4.19 - Liveability of hens during the first (——) and second (—) experiment showing the incidence of acute heat stress (HS).

Table 4.52

Probabilities of main and interaction effects on egg quality traits

(N = 384 by age)

Source of variation	Yolk weight mg/g egg	Albumen height mm	Shell weight mg/g egg	Shell thickness 0.1 mm	Breaking strength kg
Age (A)	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Diet (D)	0.877	0.326	0.905	0.649	0.520
Season (S)	0.914	0.997	**<0.001**	0.534	**0.007**
Na locus	**0.017**	**0.025**	0.554	0.762	1.000
F locus	0.577	0.644	0.149	0.609	0.693
dw locus	0.296	0.366	**<0.001**	0.214	**0.035**
A x D	0.475	0.753	0.355	0.826	0.080
A x S	**0.001**	**<0.001**	**<0.001**	**<0.001**	**0.006**
A x *Na*	0.134	0.472	0.126	0.697	0.386
A x *F*	0.302	0.484	0.130	0.083	0.295
A x *dw*	**0.041**	**<0.001**	**0.006**	0.156	0.257
D x S	0.153	0.111	0.082	0.192	0.717
D x *Na*	0.482	0.651	0.904	0.585	0.783
D x *F*	0.138	0.505	0.423	0.072	0.244
D x *dw*	0.376	0.190	0.784	0.722	0.524
S x *Na*	0.055	0.283	0.184	0.178	0.400
S x *F*	0.678	0.311	0.077	0.977	0.366
S x *dw*	0.909	0.778	0.052	0.607	0.721
Na x *F*	**0.025**	0.819	0.147	0.486	0.846
Na x *dw*	0.516	0.626	0.592	0.500	0.544
F x *dw*	0.118	0.303	0.419	0.248	0.835

Table 4.53

LS-means of main effects on egg quality traits

Factor		Yolk weight mg/g egg	Albumen height mm	Shell weight mg/g egg	Shell thickness 0.1 mm	Breaking strength kg
	μ	267.6	6.53	105.1	3.62	2.35
	SE	1.2	0.05	0.5	0.02	0.03
Age	28 wk	255.6	6.61	109.7	3.52	2.50
	40 wk	272.5	6.70	103.9	3.65	2.41
	64 wk	274.6	6.28	101.7	3.68	2.14
Diet	HP	267.7	6.48	105.0	3.62	2.37
	LP	267.4	6.58	105.1	3.61	2.33
Season	Exp. 1	267.4	6.53	107.0	3.63	2.42
	Exp. 2	267.7	6.53	103.1	3.61	2.27
Na	*nana*	264.7	6.65	105.4	3.62	2.35
locus	*Nana*	270.4	6.41	104.8	3.61	2.35
F	*ff*	268.2	6.51	105.8	3.61	2.36
locus	*Ff*	266.8	6.56	104.4	3.62	2.34
dw	*Dw-*	266.3	6.58	102.1	3.60	2.29
locus	*dw-*	268.8	6.48	108.1	3.64	2.41

Table 4.54

LS-means of interaction effects on egg quality traits

Age x Season

	Yolk weight (μ=267.7) mg/g egg		Albumen height (μ=6.53) mm		Shell weight (μ=105.1) mg/g egg		Shell thickness (μ=3.62) 0.1 mm		Breaking strength (μ=2.35) kg	
	Exp.1	Exp.2	Exp.1	Exp.2	Exp.1	Exp.2	Exp.1	Exp.2	Exp.1	Exp.2
28 wk	255.9	255.3	6.93	6.30	114.7	104.7	3.60	3.43	2.53	2.46
40 wk	275.4	269.6	6.18	7.21	101.8	106.0	3.55	3.76	2.42	2.41
64 wk	271.0	278.2	6.48	6.09	104.5	98.8	3.73	3.62	2.32	1.96

Age x *dw* locus

	Yolk weight mg/g egg		Albumen height mm		Shell weight mg/g egg	
	Normal	Dwarf	Normal	Dwarf	Normal	Dwarf
28 wk	253.0	258.1	6.86	6.36	105.7	113.7
40 wk	273.1	271.8	6.78	6.61	102.4	105.4
64 wk	272.9	276.4	6.10	6.47	98.0	105.3

Na* x *F

	Yolk weight mg/g egg	
	nana	*Nana*
ff	268.1	268.4
Ff	261.3	272.4

Table 4.55

LS-means for egg quality traits in the genetic groups

Body size type	Feathering type	Yolk weight g/g egg	Albumen height mm	Shell weight mg/g egg	Shell thickness 0.1 mm	Breaking strength kg
Dw-	*nana ff*	16.6	6.77	103.1	3.61	2.26
	Nana ff	16.7	6.46	101.6	3.59	2.35
	nana Ff	17.0	6.69	102.0	3.62	2.28
	Nana Ff	17.3	6.41	101.5	3.57	2.26
dw-	*nana ff*	15.6	6.51	110.4	3.64	2.44
	Nana ff	14.6	6.29	108.0	3.59	2.38
	nana Ff	15.2	6.64	105.9	3.62	2.40
	Nana Ff	15.2	6.48	108.2	3.69	2.40

Table 4.56

THI values and penalties to performance and survival in laying hens

THI	Safety index	Penalties to production and survival	Proposed minimum precautions
≤ 78	Normal	No influence on performance	
79 – 82	Normal to alert	Drop in egg number (up to 5 %) No major effect on egg weight or feed intake	Stressful handling [1] Drinking water [2]
83 – 85	Danger	Drop in egg number (5 % or above); Decrease in egg weight and feed intake	Drinking water [2] Sprinkling [3]
≥ 86	Emergency	Loss of birds	

[1] Stressful handling like vaccination or weighing should be avoided.

[2] Provision of cooled drinking water is ideal.

[3] If in cages, sprinkle birds (shanks, comb and wattles preferably) to decrease body temperature.

Table 4.57
Probabilities of main and interaction effects on feed conversion

Source of variation	FC (kg/dz eggs) LC I 1-52 wk	LC II 53-76 wk
Diet (D)	0.937	0.263
Season (S)	0.817	0.169
Na locus	0.194	0.905
F locus	**0.004**	**0.001**
dw locus	**<0.001**	**0.005**
D x S	0.283	0.483
D x *Na*	0.646	0.077
D x *F*	0.849	0.324
D x *dw*	0.973	0.967
S x *Na*	0.430	0.380
S x *F*	0.486	0.666
S x *dw*	0.478	**0.028**
Na x *F*	0.067	0.079
Na x *dw*	0.118	0.384
F x *dw*	0.225	0.751

Table 4.58
LS-means of main effects on feed conversion

Factor		FC (kg/dz eggs) LC I 1-52 wk	LC II 53-76 wk
	μ	1.70	2.00
	SE	0.01	0.03
Diet	HP	1.70	1.97
	LP	1.70	2.04
Season	Exp. 1	1.70	2.04
	Exp. 2	1.70	1.98
Na	*nana*	1.69	2.00
locus	*Nana*	1.71	2.00
F	*ff*	1.67	1.91
locus	*Ff*	1.72	2.10
dw	*Dw-*	1.79	2.08
locus	*dw-*	1.61	1.93

Table 4.59
LS-means of on feed conversion in the genetic groups

Body size type	Feathering type	FC (kg/dz eggs) LC I 1-52 wk	LC II 53-76 wk
Dw-	***nana ff***	1.80	2.08
	Nana ff	1.75	1.92
	nana Ff	1.78	2.13
	Nana Ff	1.82	2.20
dw-	*nana ff*	1.56	1.84
	Nana ff	1.59	1.81
	nana Ff	1.61	1.96
	Nana Ff	1.68	2.10

Table 4.60
Egg size classification, as % of marketable eggs

Body size group	Laying cycle I Small <47.3 g	Medium 47.3 to 54.2 g	Large 54.3 to 61.4 g	E-Large, Jumbo >61.5 g	Laying cycle II Small <47.3 g	Medium 47.3 to 54.2 g	Large 54.3 to 61.4 g	E-Large, Jumbo >61.5 g
				Experiment 1				
Dw-	0.3	3.6	32.4	63.7	0.0	0.1	8.6	91.3
dw-	2.8	21.3	49.0	26.9	0.0	2.3	27.4	70.3
				Experiment 2				
Dw-	3.3	10.2	31.3	55.2	0.0	0.3	16.6	83.1
dw-	12.2	23.2	43.0	21.6	0.0	7.4	44.9	47.7

Table 4.61

Summarised economic indicators in the genetic groups [1]

	Dw-				*dw-*			
	nana ff	*Nana ff*	*Nana Ff*	*Nana Ff*	*Nana ff*	*Nana ff*	*nana Ff*	*Nana Ff*
LAYING CYCLE I								
Contribution margin, %	23.3	24.3	22.0	21.5	30.4	29.0	28.1	26.0
Break-even output, % total production	62.6	60.0	64.6	64.6	55.1	56.1	57.9	61.0
Break-even feed price, % current price	137.3	139.3	134.7	133.6	155.0	153.0	150.9	145.7
Break-even egg price, % current price	76.7	75.7	78.0	78.5	69.2	70.6	71.5	73.6
Impact of feathering on gross margin, %	0.0	3.8	8.7	4.4	0.0	4.0	0.9	0.7
Impact of grading on gross margin, %	38.8	40.4	42.4	45.0	5.1	6.8	11.0	11.0
LAYING CYCLE II								
Upper limit of profitability, wk	66	69	61	53	60	62	57	56
EXP. 2/EXP. 1 [2]								
First laying cycle 1-52 wk, %	+0.3	+23.7	-5.8	+9.3	-26.7	+13.8	-22.1	-21.4
Both laying cycles (1-76 wk), %	+0.3	+22.4	-2.4	+6.5	-14.5	+11.9	-14.2	-15.1

[1] Based on data presented in Annexes 2 to 6.

[2] Based on gross margin per hen housed

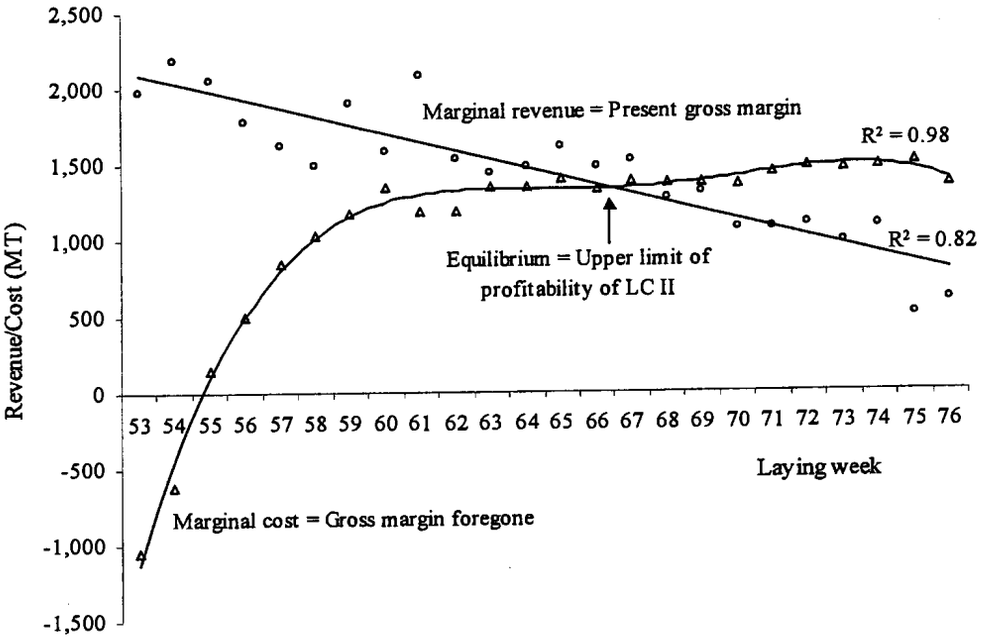


Figure 4.20 – Profitability of the second laying cycle in the normal hen (*nana ff Dw-*) (ρ□ observed values; — trendline)

Table 4.62

Comparative financial analysis of the genetic groups in the first cycle [1]
(as % deviation from the control type *nana ff Dw-*)

	Dw-			*dw-*			
	Nana ff	*nana Ff*	*Nana Ff*	*nana ff*	*Nana ff*	*nana Ff*	*Nana Ff*
Feed cost per surviving hen	+ 1.7	+ 0.8	+ 4.7	- 29.2	- 27.5	- 28.5	- 25.9
Margin over feed cost per surviving hen	+ 4.4	- 3.8	- 3.8	- 0.1	- 3.2	- 6.5	- 11.0
Gross margin per hen housed	+ 6.1	- 0.7	- 7.3	+ 14.8	+ 8.8	- 0.7	- 3.1
Gross margin per hen housed area	+ 6.1	- 0.7	- 7.3	+ 49.3	+ 41.5	+ 29.2	+ 25.9

[1] Based on scenario 1 (see Annex 2)

5 DISCUSSION

In the tropics, poultry production is influenced by direct and indirect adverse effects of heat stress and birds are unable to maintain optimal reproductive and productive functions. Breeding strategies using major genes that can improve tolerance to elevated temperatures might be adopted along with appropriate management techniques. The existence of different gene x environment interactions recommends the adaptability of such genes being evaluated at each specific location. In addition, as egg production in Maputo is being menaced by cheap imports from neighbouring countries, impeding further development of the industry, the breeding strategy should envisage the production of eggs at lower cost and higher return on capital invested.

The present work was aimed at testing whether the major genes for feather reduction (naked neck) feather curling and reduction (frizzle) and body reduction (dwarf) significantly contribute to the biological and economic efficiency of a medium heavy layer strain in the climatic conditions of Maputo, using standard and sub-standard nutrient regimes.

5.1 Productive adaptability of major genes

None of the feather-reducing genes (*Na* or *F*) evidenced superior egg production, even in the periods with higher temperatures, though the first gene excelled in terms of biological efficiency and productivity. Positive effect of the *Na* gene on productivity was earlier reported by Rauen *et al.* (1986). It appears that the cooler nocturnal temperatures eased the effect of diurnal heat strain on birds in this natural cyclic environment, conceding to feather reduced birds no significant productive advantage. This confirms previous findings that both genes evidence better productive adaptability in conditions of constant high ambient temperatures, but show no consistent superiority in less stressful environments (Rauen *et al.* 1986; Haaren-Kiso, 1991).

Interestingly, the frizzle gene was associated with greater egg weight throughout the first experiment. Such effect was apparently independent of the climate and was not reported in the second and hotter experiment. This suggests that the known favourable influence

of the gene on egg weight in conditions of prolonged heat stress (Haaren-Kiso *et al.*, 1992, 1994) is not absolute. These authors explained the higher weight of eggs laid by frizzle birds as being a specific side effect of the gene. In fact, our findings seem to point out that it was associated with the larger body weight of hens rather than with increased synthesis of egg components under warmer environments.

Feed intake was increased in both *Na* and *F* genes, which is known to be advantageous in withstanding the indirect effects of high temperatures on both egg number and egg weight. However, especially in the case of the latter gene, such increased consumption was not compensated with equivalent superior productivity, resulting in poorer efficiency of feed utilisation, measured either per mass or per number of eggs. Furthermore, the association of both genes, irrespective of the *dw*-locus, was particularly adverse in the second experiment due to the additional reducing effects of the moult on production, conferring to the birds with such genetic configuration the poorest feed efficiency and conversion.

The significant depressing influence of the dwarf gene on such quantitative traits as egg number (-18 %), egg size (-8 %) and egg mass (-25 %) was expected from previous studies. In overall terms, the magnitude of the reduction agrees well with the reports of Mérat (1984), Mukherjee *et al.* (1986) and Horst & Becker (1991). The interaction with season observed in various periods, however, indicates that the early sexual maturity and the resulting lowered body weight as well as the occurrence of the moult in the most productive phase of the cycle were particularly adverse to the genotype in the second experiment. Although summer dwarfs started laying 20 days earlier than the winter counterparts, egg number was reduced 10 %, egg weight was lighter by 5 %, egg mass decreased 13 % and the profitability per hen housed was 14 % lower.

On a long-span evaluation, however, the effects of the moult were attenuated, both in productive and economic terms, as a result of the outstanding persistence observed in the final weeks of the first year and in the second cycle (Table 4.22 and Fig. 4.11). No comparable post-moult persistence was seen in the oldest moulted hens of the first experiment. This is in accordance with Bell & Adams (1992), who reported a

significantly lower decline in the production of the younger flocks during the first 30 weeks after the moult. Despite these considerations, it is on every account surprising that the rate of lay was maintained constant under the high temperatures of the summer. This fact suggests that, in addition to the boosting influence of the moult, dwarf hens might have an increased ability to withstand the effects of the climate. In fact, more stable intensity of laying and smoother and greater egg weight increase over time during the summer in the first experiment hint possible higher tolerance of the genotype to the effects of heat stress.

The characteristic increasing effect of the sex-linked dwarfing gene on productivity (number of eggs per $kg^{0.75}$) was also observed in the present study. The effect was general, since it occurred in both cycles and experiments, yet moult reduced the margin over the normal genotype in the second experiment. This is in good agreement with the report of Horst *et al.* (1996) based on an international field test. Furthermore, our values closely follow those originating in tropical countries. The increasing effect of the gene on biological efficiency (egg mass per $kg^{0.75}$), however, could only be observed in the first cycle of the first experiment. Although the interference of moult should not be ignored, it appears that the lower biological efficiency in the second and more stressful experiment resulted mostly from reduced egg weight associated with lowered body weight of the birds. These results are somehow different from those measured by Haaren-Kiso (1991), as this author obtained lower biological efficiency in dwarfs kept under temperate conditions (18-20 °C) while similar in a controlled warm environment (32 °C). Such differences reflect the effects and express the importance of genetic interactions with the environment.

Another characteristic feature of the dwarf gene, that of being more efficient in feed utilisation than the normal-sized birds was observed in this work likewise. Dwarfs required less feed either per unit of egg mass or per dozen eggs produced, irrespective of the environment and different maintenance requirements between seasons. In general, these findings are in good agreement with earlier research, but the magnitude of the difference to the normal birds was much lower than the reported by Katangole *et al.*

(1990) and Haaren-Kiso (1991) for birds with similar genetic background as ours in either temperate or warm climates.

The increased survival rate of small-bodied birds resulting from lowered metabolic rate and lowered heat production in a situation of acute heat stress was demonstrated in the first experiment as almost three times less dwarfs died. Bell *et al.* (1983) also reported higher survivability of dwarfs compared with normal hens. However, the results in the second experiment suggest that the higher survivability of dwarfs was not absolute, and two factors could eventually explain the similar mortality observed in both body size groups. First, non-dwarf hens were considerably lighter and thus could better tolerate the elevated temperatures. Second, acclimatisation might have harmonised the response of hens to acute heat strain.

The lower mortality of birds carrying the *Na* gene in the second cycle indicates increased thermotolerance to the stressful conditions prevailing during the first half of Exp. 2 and the second of Exp. 1. It appears that the greater sensible heat loss of naked neck birds under high temperatures became advantageous later in their productive life, when a higher heat load resulting from larger body mass had to be dissipated. Superior liveability of naked neck birds in conditions of constant heat stress was earlier reported by Rauen *et al.* (1986).

5.2 Growth and sexual maturity

The significant depressing effect of high ambient temperatures on growth of pullets experienced in this study agrees well with the extensive reports in literature (Marsden *et al.*, 1987; Njoya, 1995; Yahav *et al.*, 1996). The effect of high temperature on the final body weight (18 wk) was particularly accentuated when birds were subjected to a hot climate in the last stages of growth (Exp. 2). Although food consumption was not measured during the growing period, an indirect effect of temperature through reduced feed intake might have occurred in that experiment, despite the greater feeding opportunity provided by the longer photoperiod. Apparently, compensatory growth

occurred when pullets were kept under a mild environment following an exposure to higher temperatures early in life and fed without any natural imposed restriction, yet in shorter days (Exp. 1).

Egg laying is the ultimate goal for rearing a layer pullet. Therefore, a high degree of uniformity rather than maximised weight gain should be the most important target of a breeder, provided that a minimum body weight necessary for optimal production and feed utilisation, as well as satisfactory egg size is achieved at the end of the growing phase. Furthermore, research has demonstrated the importance of the pattern of growth over body weight at the end of rearing on the pullet's subsequent performance (Kwakkel, 1994). Nevertheless, it is interesting to note that, in the present study, none of the feather-reducing genes (*Na* or *F*) induced superior growth of the pullets during the periods with higher ambient temperatures, i.e. at the beginning of the first and at the end of the second experiment, contrasting with the findings of Abdellatif & Horst (1994). This suggests that the stressful effect of diurnal elevated temperature on the body thermal condition of the birds was efficaciously compensated by the nocturnal amplitude of temperature, inhibiting the genes taking advantage of their increased ability to dissipate heat and achieve better growth response. Apparently, the higher sensible heat loss of naked neck females represented no disadvantage for growth at lower temperatures during the first two months of the second experiment. In contrast, increased heat loss of frizzle birds, resulting from the higher degree of de-feathering, was associated with lowered body weight during the same period, which was maintained until the end of the growing phase. This confirms the greater flexibility of the *Na* gene in thermoregulation reported by Touchburn *et al.* (1980) as well as the conclusions of Eberhart & Washburn (1993) and Yahav *et al.* (1998), that the thermoregulatory advantage of feather-reduced birds is not general and in some cases small, especially under cyclic temperatures. The results also indicate that environmental temperature was not a constraint to the growth of normal feathered birds.

Expected differences in body weight of dwarf and normal birds are in accordance with previous reports (Guillaume, 1976; Ricard, 1976). Characterisation of growth of both genotypes differed depending whether it was expressed as actual body weight (Fig. 4.5)

or as a proportion of body weight attained at the first oviposition (Fig. 4.7). While the first shows a clear differentiation of size between the groups after the second week of age, the latter indicates that dwarf and non-dwarf birds can have the same pattern of growth to sexual maturity, provided that an apparently required threshold photoperiod is reached (discussed in section 5.5). Similar relative growth to maturity was also reported by Zelenka *et al.* (1986) for dwarf and non-dwarf birds with the same genetic background.

High temperature and reduced body weight are known to delay sexual maturity (Cowan & Michie, 1983; Kyarisiima & Balnave, 1996), which did not occur to the pullets grown in the second experiment. Apparently the gradually increasing daylight length exclusively induced the acceleration of reproductive tract development and thus the advancement of onset of lay in this experiment. In terms of photoperiod and feeding opportunity, the natural environments of each season herein studied present reasonable similarities with the controlled conditions used by Proudfoot and Gowe (1973). Their light-decreasing full-fed birds were sexually immature for a further 15 days in comparison with the light-increasing feed-restricted ones. It might than be reasoned that the hypothalamo-pituitary axis of the birds in the second experiment was sensitive to photostimulation earlier in their life as compared with their siblings in the first experiment, and that a certain degree of feed restriction increased the response of the reproductive system to photostimulation, as also suggested by Dunn & Sharp (1990).

In the second experiment, the minimal body weight required for the onset of lay was 1,300 g and 920 g in normal and dwarf pullets, respectively. Birds in the first experiment reached these weights at approximately 14.5 (*Dw*-) and 15.5 (*dw*-) weeks of age, but the first ovipositions were seen to occur only four weeks later. This confirms that body weight *per se* was not a good determinant of sexual maturity in the pullets, which contrasts with the hypothesised by Dunnington & Siegel (1984). However, the results provide some evidence that beyond a threshold age the onset of lay was weight-dependant, given the weak but different from zero correlation between body weight and age at first egg in each experiment (-0.11 in Exp. 1; 0.11 in Exp. 2). Moreover, the negative relationship observed in the first experiment would indicate that a threshold

weight (or weight range given the great individual variability) was essential for the start of egg production, agreeing with Bornstein *et al.* (1984). The birds which grew more rapidly in the early part of the rearing period (Fig. 4.6, Exp. 2) in comparison with those with higher growth rate in the later part (Fig. 4.6, Exp. 1) advanced sexual maturity in a similar manner to that described by Lewis & Perry (1996). This stresses the greater importance of growth rate and the pattern of growth over the arrival at a particular fixed weight in the timing of sexual maturity, as earlier suggested by Glass *et al.* (1976) in rats and confirmed by Dunn & Sharp (1992) in dwarf broiler breeders and Kwakkel *et al.* (1991) in egg-type pullets.

The very low or nil correlation between onset body weight and the weight of the first eggs laid by the late-maturing and heavier pullets (Exp. 1) in contrast with the higher correlation observed for the early- maturing and lighter pullets (Exp. 2) shows that, in general terms, the former trait was also a poor indicator of the latter. These findings are consistent with earlier and recent work of Christmas *et al.* (1979) and Kershavarz (1998), who reported a disproportion between the body weight of heavier pullets, winter-maturing or raised under a step-down light regime, and the weight of their first eggs in comparison with lighter, summer- or early-maturing pullets. The lower initial egg weight of either dwarf females in the second experiment or frizzle birds allocated to the HP diet was associated with lighter body weight. The lower onset body weight of frizzle birds allocated to the diet with higher protein content derived from a coincidental lower weight at housing, since allocation of birds to diets was done randomly. This unexpected occurrence affected the weight of the eggs produced during the first two months. A strong relation of initial egg size and chronological age was also reported by Kling *et al.* (1985) and Leeson *et al.* (1991).

The equal proportion of onset weight at 8 weeks of age in normal and dwarf confirm the similar rates of gain between the groups until attainment of sexual maturity, as earlier discussed. Conversely, the values obtained at 38 weeks of age show a lower rate of growth in dwarfs from the start of lay to mature age, reflecting restrictions imposed on body development during laying. Such restrictions could be deriving either by higher nutrient partitioning for greater egg production (Exp. 1) or limiting nutrient intake

associated with lighter body weight (Exp. 2). Therefore, body weight at sexual maturity was more closely associated with juvenile than with mature weight. These findings are in full contrast with those reported by Dunnington *et al.* (1983) and Brody *et al.* (1984). However, these authors worked with normal and dwarf populations under a long-term selection for high and low body weight at 56 days, which might explain the different results obtained. Differences in the proportion of onset body weight at juvenile age between seasons are consistent with the already demonstrated younger physiological age of birds in the first experiment. The lower proportion of onset weight observed in birds fed the low protein diet resulted from lowered body weight at 38 weeks, as farther discussed.

Lowered body weight at the end of the rearing period and at sexual maturity persisted throughout the laying phase, indicating a carry-over effect and absence of compensatory growth, similarly to the reported by Robinson *et al.* (1995) and Keshavarz (1998). Body weight development of females in the second experiment was further restricted in the first stages of laying since high temperatures prevailed during early production, as opposed to their replicates in the first experiment, which were kept under milder conditions.

5.3 Climatic season

The effects of heat stress on early production in the second experiment were severe, when compared with the results obtained during equivalent physiological stage in the first. In the latter experiment, pullets were exposed to a gradual increase in ambient temperature as early as 10-12 weeks of age and a certain degree of acclimatisation might have been induced. However, if physiological changes occurred during growing in response to hot climate, they could not overcome the detrimental influence of high temperatures on egg laying during the first phase of the cycle. This agrees well with the early findings of Stockland & Blaylock (1974) and with more recent work of Njoya & Picard (1994), that rearing pullets at high ambient temperatures does not seem to

acclimatise them to hot environments during laying any better than rearing under temperate conditions.

The favourable influence of a mild climate and increasing daylight length during the first months of production in the first experiment were added to the beneficial effects of late sexual maturity and higher body weight, resulting in more and larger eggs produced in the first cycle. This contrasted with the stressful climatic conditions and diminishing daylight length prevailing during equivalent period in the second experiment. Lowered body weight resulting from early maturity also played a negative role both on egg numbers and egg weight, agreeing with Proudfoot & Gowe (1974) and Leeson *et al.* (1991). Furthermore, the milder environment in the following stages of the cycle did not fully compensate for such detrimental influence on yearly production. However, the depressing influence of higher temperatures and shorter photoperiod on egg number during the first cycle was confounded with the effects of the mid-cycle moult. This was especially true among the dwarfs, as the degree of impairment was twice as much that observed in the non-dwarf hens. Conversely, persistency of lay was higher in the second and hotter experiment, independently of the effect post-moult might have exerted, confirming earlier findings of Marsden *et al.* (1987) and Njoya (1995). These authors proposed that greater persistency at higher ambient temperatures derived from the effect of acclimatisation or from lower metabolic rate caused by reduced rate of thyroxine secretion.

Voluntary feed intake was reduced by the higher temperatures in the second experiment, independently of the different body weight and hence different maintenance requirements of the hens. A quantitative assessment of such effect might be done comparing similar physiological stages in both experiments during a period with extreme temperature differences. Our calculations account that absolute feed intake was reduced 1.4 % for each one-degree rise in temperature in the first eight weeks of production in the second experiment relatively to the first. Such magnitude of decrease is similar to the reported by Payne (1966) in equivalent temperature ranges. As the laying year progressed, the diminishing reduction in feed intake observed was associated with less extreme temperature differences.

In overall terms, both measures of efficiency, either biological or of feed utilisation were depressed in the cycle starting in summer. However, due to the confounding influence of the moult, the true seasonal effect should be analysed separately in the non-dwarf hens. In doing this, there is evidence that the yearlong biological efficiency of hens was equivalent, no matter the starting climate or body weight of the birds, yet it should be mentioned that the mass of eggs produced, total or per metabolic weight, was significantly depressed in those periods with higher temperatures. Conversely, the reducing effect of elevated temperatures on feed efficiency occurred similarly in both size groups, indicating a net climatic influence, with the effect of the moult on this trait, if any, being small. Interestingly, the degree of decrease in egg numbers during the second experiment was proportional to the degree of reduction in feed intake, originating a precisely equal amount of feed consumed per dozen eggs in both climatic seasons. Comparable consequences of long-term exposure to heat stress on biological and feed efficiencies were reported by Haaren-Kiso (1991). Oppositely, de Andrade *et al.* (1977) reported better feed efficiency and conversion in cyclic elevated temperatures (31 °C) than in moderate environments (21 °C). Reasons behind such differences might lie on the shorter period and/or on the physiological rather than chronological scale of measurements used in their study or simply on the fact that results obtained in simulated environments do not reproduce the real variations experienced by laying hens in practical conditions.

Undoubtedly, the second experiment imposed more stress on performance than the first, since high temperatures prevailed during the early and more crucial stages of the cycle. The general decrease in consumption, production traits and body weight gain experienced in this study at hot ambient temperatures confirms previous reports (Njoya, 1995; Kyarisiima & Balnave, 1996). Comparing the results achieved by the normal feathered non-dwarf hens (the control group) between experiments might give a basic quantitative indication of the seasonal effects on productive and economic performance. This genotype is, by definition, less tolerant to the effects of heat and, according to our findings, was apparently unaffected by the moult. In the first experiment, the laying year was shorten by 10 days due to late maturity, yet each normal hen produced 15 eggs

more, corresponding to 700 g of egg mass, and consumed only 6 g/day more than a counterpart in the second. Therefore, it might be reasoned that the penalty for starting egg production during the summer would correspond to a 5 % decrease in the number of eggs produced (either in 52- or 76-wk cycle) and a 17 % (in 52-wk) or 12 % (in 76-wk) reduction in the margin over feed cost in comparison with production initiated in wintertime. The profitability per hen housed, however, would be similar in view of the lower mortality occurred in the second experiment.

Mortality occurred only when extremely high ambient temperature was combined with very low relative humidity. Such specific combination of stressful environmental factors probably caused a sharp increase in the birds' core temperature beyond survival limits. This would be in line with the results of Yahav *et al.* (1995), who recorded maximum rectal temperatures in females at 35 °C and 40-50 % RH in comparison with those kept at the same temperature but at RH values above that range. Two factors might have contributed to the higher mortality occurred in the first experiment. First, the temperature associated with the death of birds was higher (HS1, 43 °C) and thus more lethal than the two occurrences in Exp. 2 (HS2 and HS3, 39.5 °C). Second, the birds had not been exposed to high temperatures in the preceding periods, whereas those in the second experiment had been under a hot weather for about five months at the time of the first hot spell. The latter fact suggests an increased tolerance of the hens to acute heat stress induced by acclimatisation.

5.4 Dietary protein

Birds fed the low-crude protein diet sustained egg production at similar levels to those fed the higher protein in both experiments, but were unable to maintain comparable egg weight throughout the first cycle in the second experiment. As earlier mentioned, the latter experiment was characterised by hot weather during the most crucial part of the first cycle, as well as by the occurrence of a natural moult immediately after the summer. The first factor reduced feed and nutrient intake and the second might have increased the protein (or amino acid) requirements for feather renewal and egg laying resumption. In

parallel, relative body weight increase of the birds in this very same experiment was higher, which certainly altered the partition of nutrients for production. Birds fed the LP diet consumed approximately 13 % less protein per day though equivalent (estimated) amounts of essential amino acids than their siblings in the HP diet. One of the major nutrients controlling egg weight and component mass is methionine (Roland *et al.*, 1996), and about 8 mg of this amino acid is required for each 1 g egg content produced (Schutte *et al.*, 1994; Harms & Russel, 1995). In both experiments, but with expressiveness in the second, birds were fed less methionine than the required according to the mass of egg content they produced. Whether the size of the eggs laid by hens fed the LP was reduced by insufficient protein intake or any critical amino acid is, however, difficult to establish. Interestingly, Koelkebeck *et al.* (1991) found a significant influence of methionine supplementation on post-moult egg weight in the fall and in winter but not during the summer.

The sustenance of egg production by hens fed the low protein diet in comparison with their counterparts under the higher protein regime was done at the expense of lower gains in body weight, regardless of the environmental temperature. Furthermore, older hens (31-52 wk) fed the LP diet in the first experiment sustained production by mobilising body reserves, as indicated by the weight loss, following a period with high temperatures and reduced feed consumption. This is in accordance with Scott & Balnave (1991), who concluded that, within limits, a hen might mobilise body reserves to meet the differences between intake and output of eggs.

If the reason for decreased egg weight and body weight loss was related to nutrient(s) deficiency, resulting from either insufficient consumption or decreased digestibility, hens fed the LP diet made no apparent attempt to compensate for it by significantly increasing the amount of feed consumed. They would not possibly increase intake during the summer months, but a higher consumption would be expected during the periods with milder temperatures and/or higher nutrient requirements. In fact, consumption of LP diet was 2 % higher in the periods elapsing between 1-8 wk in the first experiment (mild weather) and 31-52 wk in the second (post-moult). Such increase, however, was negligible and clearly insufficient. Diets were formulated to be isocaloric. Yet, a certain

energetic imbalance might have occurred and the real ME content of the LP diet could have been higher. If this was the case, it appears that feed intake was energy-regulated and metabolizable energy became the refraining factor, in view of the need to reduce endogenous heat production under temperatures which, despite being mild, were on the fringe of the upper limit of the thermoneutral zone of the birds. This would be in line with the report of Peguri & Coon (1991) that high temperatures impose limits to metabolizable energy intake in layers at density levels above 2,650 kcal/kg.

From the standpoint of protein 'requirements' our results seem to indicate that daily intakes in the range of 18 to 20 g in normal hens and 13 to 15 g in dwarfs supported equivalent levels of egg production and maintained egg weight, but did not permit comparable accretions in body weight. Daily intakes below the minimum reduced egg weight whereas decreased body weight gains occurred below the maximum. Therefore, those values provide evidence that, in the conditions of the present study a diet containing 144 g protein/kg and supplemented with methionine and lysine sustained laying performance almost identical to that achieved on a diet containing 162 g protein/kg. However, the comparison of our results to those described by Schutte *et al.* (1983) and Leeson & Caston (1996), both working with similar crude protein (14 and 16.5 %) but higher methionine (0.42-0.47 %) levels, suggests that an increase in methionine content of the LP diet could have been effective in sustaining egg weight as well, in conditions of decreased feed intake or increased requirements. These results give an indication that the concentration of dietary protein should be considered when determining the requirements of laying hens for sulphur amino acids, agreeing with Calderon & Jensen (1990). On the other hand, they justify the common recommendation that diets of higher nutrient concentration should be considered for laying hens under severe temperature stress (Marsden *et al.*, 1987; Njoya, 1995). Whether to increase methionine or not, however, would depend on the specific objectives of the enterprise regarding the size of the eggs and ultimately on a cost-benefit criterion.

Reports in literature give account of a higher egg weight reduction by low dietary protein content in dwarf hens, and suggest a greater protein (or methionine) requirement, especially in lighter laying strains (Guillaume, 1976; Cherry *et al.*, 1978; Bell *et al.*,

1983). The results in the first experiment, with equivalent egg weight produced by dwarfs in both diets, give no evidence of diminished protein or amino acid efficiency. Conversely, in the second experiment the reducing effect of the LP diet on egg weight among dwarfs was two-fold that observed in normal hens. Dwarf females in the first experiment were 5 % heavier and consumed 6 % more feed and concomitantly more nutrients per unit of metabolic body weight than their counterparts in the second, which might justify the different responses to dietary protein observed between experiments. In addition, nutrient deficiency in the second experiment might have been boosted by increased requirements during and after the moult, as explained earlier. It appears then that the productive response to the protein content of diets of medium-heavy dwarfs depends mostly upon the body weight and level of consumption of the birds, which confirms that both traits must be considered when determining the protein (or amino acid) requirements of dwarf egg-type layers.

An opposite response to the protein content of diets was observed in genotypes at the *Na* locus. The higher egg mass produced by naked neck birds fed the LP diet in the first cycle of both experiments resulted from either increased egg weight (1-8 wk; 31-52 wk) or egg number (9-30 wk) and was achieved with equal level of consumption to that of siblings fed the HP diet. Although a positive effect of the *Na* gene on egg weight and egg mass was described in different works (Rauen *et al.*, 1986; Bordas & Mérat, 1992), the more pronounced the higher the ambient temperature, the genetic-nutrition interaction herein observed is so much the more interesting as lower egg weight and egg mass was produced by naked neck hens in comparison with normal counterparts under the HP regimen. Moreover, the effect occurred in non-dwarf and dwarf genotypes alike. Effects of dietary protein on the performance of naked neck layer hens have not been reported as to our knowledge, but information exists on the growth of broilers. Touchburn *et al.* (1980) reported lower nitrogen retention in female *Nana* chicks when fed a diet with higher protein content. Pesti *et al.* (1994) demonstrated that *Nana* birds were more efficient at low sulphur amino acid levels, though reported similar quantitative protein requirements. Later, Pesti *et al.* (1996) observed that body weight of *Nana* broilers excelled that of normal birds only at the lowest protein level ranging from 111 to 205 g/kg. The reason for the superior productive response of the genotypes at the *Na* locus to

the LP diet is not clear-cut. It might in fact be associated with higher retention of nitrogen related to synthesis of essential amino acids under low dietary protein. However, it might also be explained by the energy to protein ratio of the diet under question. Energy maintenance requirements of naked neck birds are higher in comparison with normal feathered chicken due to greater heat loss from the exposed skin areas, with food intake being increased to provide extra metabolic fuel for heat production (Yahav *et al.*, 1998). Considering that the true metabolizable energy content of the LP diet could have been higher than the planned, as earlier mentioned, it follows that less protein was needed as an energy source for maintenance and more might have been directed for egg production.

5.5 Natural moult

In avian species, moulting is a natural process of feather renewal prior to migration, shorter days or cooler weather. The process is under hormonal control and is accompanied by the regression of the reproductive organs and the cessation of lay, lasting for 3 to 4 months. Normally, wild chickens moult once a year and as they produce but a few eggs, the moult is not associated with the laying cycle. Oppositely, domestic chickens have been bred for high egg production, and under normal circumstances they do not go through a complete moult until the end of a long and intensive laying period (North & Bell, 1990). In commercial flocks, hens are recycled by forced moulting, usually induced by diet and light manipulation. Moult inducing methods and their effects on subsequent performance are well documented in literature (Brake, 1993; Hussein, 1996), but fewer works describe natural moulting in commercial layers (Herremans, 1988). Moreover, no previous occurrence of a natural moult in the experimental hybrid strain studied was reported (P. Horst, personal communication, 1999).

The results suggest that the observed moult was a photoperiod-induced process. It started at the onset of autumn when photoperiod had decreased to its yearly minimum. The phenomenon was neither circannual nor related to the chronological age or physiological stage of the hens. Nonetheless, both the impact of moult on egg production and the

ability of hens to fully resume laying after the moult were influenced by their chronological age, as greater depression but also higher recovery was seen in the younger and more productive hens. The effects of moult in the older group could have been to a certain extent confounded with the natural reproductive senescence of the birds. This would explain the higher percentage of non-laying normal size hens as well as the occurrence of hens showing permanent regression of production in the post-moult period.

Although de-feathering was observed in birds of both body size groups, the effects on egg production were mostly circumscribed to birds carrying the sex-linked dwarfing gene. In addition, the sexual maturity of dwarfs and especially that of the feather reduced ones was delayed beyond normal expectations in the first experiment. Moult is under hormonal control and both plasma prolactin and luteinizing hormone (LH) are lowered in moulting females (Scanes *et al.*, 1979). It might then be reasoned that the short photoperiod (less than 11 hours) prevailing at the beginning of autumn triggered a reduction in the basal concentrations of the hormones involved in the induction of moult and regression of the ovary in the dwarf birds. There is no evidence in literature of a consistent greater sensitiveness of the dwarf females to light. Longer delay in reaching sexual maturity was observed by Proudfoot *et al.* (1984) in dwarf birds light stimulated later than earlier in life in comparison with normal hens. The work of Mérat *et al.* (1988) gives account of a slight advantage of medium-size dwarf laying hens in long photoperiods, whereas Dunn & Sharp (1990) reported that broiler dwarf pullets had a shorter critical daylength for LH release than the normal size egg-layer strain studied. In a latter work, Dunn & Sharp (1992) indicated that in dwarf broiler breeders, photoperiodic history, and therefore the development of photorefractoriness, is less important than age *per se* in maintaining intensity of egg laying at older ages. Forssido & Jaap (1975) were the only authors, as to our knowledge, reporting the effects of moult in a layer-type dwarf population. They found lower de-feathering rate and higher decrease in egg production levels followed by longer period to resume pre-moult production in egg-type dwarfs as compared to small-bodied normal hens after a forced moult.

5.6 Egg quality

Yolk weight and its relative proportion in the whole egg are known to increase with the age of the hen (Yannakopoulos *et al.*, 1994). In overall terms, our results are in good agreement with these findings. However, in the first experiment non-dwarf hens only partly followed such trend, as their yolk proportion was equal in the second and third age analysed. This indicates that egg weight increased by means of an increase in the albumen and suggests that a deceleration in yolk increase occurred in association with elevated temperatures prevailing between those two periods. In the second experiment and between 28 and 40 weeks of age, birds also experienced high temperatures, yet similar disturbance on the relative growth of yolk was not observed. It appears that older non-dwarf hens became more susceptible to the environmental heat stress and that their ability to mobilise the energy and nutrients needed for yolk deposition was diminished, which would agree with Lillpers & Wilhelmson (1993). Elevated temperatures did not affect yolk synthesis in the dwarfs, at least to the same extent as in the non-dwarfs. These findings confirm the greater depressing effect on egg weight at older ages in the heavier non-dwarf population and a better ability of lighter dwarf birds to withstand a temperature challenge and to sustain yolk and egg weight, as reported by Horst & Petersen (1979) and Horst & Becker (1991).

Albumen height as well as shell proportion and thickness were seen to decrease with increasing temperature, confirming earlier research (Ahvar *et al.*, 1982; Grizzle *et al.*, 1992) and to recover when the temperature decreased. However, breaking strength decreased throughout, independently of the influence temperature might have exerted. Similar results were reported by Ahvar *et al.* (1982). The poorer quality of the thick albumen observed in naked neck hens is quite surprising and could not be fully confirmed in literature. Mukherjee *et al.* (1986) reported a 12 % reduction in albumen height in naked neck hens of a lightweight breed but a converse increase in the medium strain.

Dwarf hens had better shell quality at all ages than their normal counterparts, as indicated by the greater proportion of shell and higher breaking strength. Our results are

contrasting those of Cherry *et al.* (1978), who found similar shell percentage and those of Horst & Petersen (1981) and Katangole *et al.* (1990), who found similar or decreased breaking strength in dwarf birds. However, the superior quality of the eggshells produced by dwarfs might explain the lower egg loss due to breakage (Annex 2), which confirms reports by Mérat (1994) and constituted an economic asset of the genotype. The dwarfing gene was also associated with lower decrease in the quality of the albumen at older ages and under high temperatures, similarly to the reported by Horst & Petersen (1981).

The higher percentage of cracked eggs observed in the frizzle hens (Annex 2), which was attenuated in the frizzle dwarfs, could not be associated with decreased shell quality. It appears to be of mechanical origin, probably resulting from more nervous and restless behaviour, confirmed by the occurrence of pecking in these genotypes.

5.7 Economic efficiency of the genetic groups

The analysis of the potential profit the farmers would be able to obtain per hen in equivalent conditions to this study indicates that normal feathered dwarfs (*nana ff dw-*) followed by naked neck dwarfs (*Nana ff dw-*) and naked neck non-dwarfs (*Nana ff Dw-*) were the only genotypes to evidence advantage over the normal type (*nana ff Dw-*). This would apply for gross margin per hen housed, i.e. when the net cost of the pullet and mortality were taken into consideration and for the scenario using a single selling price. If there were a premium for the larger eggs, results would be quite different. Under these circumstances, only naked neck non-dwarfs could compete with the normal feathered non-dwarf type of hen. In addition to the higher return on capital invested in feed and replacement pullets in comparison with the normal layer, all the three genotypes allowed production being financially feasible for at least two months beyond the first year. This would be advantageous to the target farmers in Maputo, as they often extend production beyond the conventional 12 or 13 months of lay before flock recycling.

The objectives of the present study presupposed the biological and economic evaluation of the birds to be averaged over climatic seasons, and the comparison of the financial results was carried out accordingly. The starting month of both experiments was chosen in order to get extreme temperature and relative humidity differences during the most relevant physiological stages. As it was expected, productive and concomitantly, economic performance of birds varied greatly between seasons. As an example, in the conditions of the first experiment and considering a single selling price for eggs, the gross margin per hen housed obtained with a normal feathered dwarf was 31 % higher than that of a normal hen, while in the second the genotype equalled the control birds (data not shown). Conversely, naked neck genotypes, non-dwarf and dwarf alike, were not favoured in the first experiment, whereas in the second both achieved a gross margin 16 % above that of the normal birds (data not shown). Despite these considerations and the time limitations of the present study, the demonstration of the economic superiority and relevance of the three genetic groups identified relatively to the normal type of layer seems reliable.

The economic efficiency of frizzle and naked neck frizzle either non-dwarf or dwarf was not favoured in the specific natural climatic conditions of Maputo and could not compete with that of a normal type of layer on a commercial basis, even in the event of differentiated egg prices. The extra revenue farmers might get with the sale of spent females carrying the frizzle gene, which would make financially feasible the use of both size types in the peri-urban production system, should be viewed as contingent and depending upon the demand of such market niche. However, since production and hence financial results of single or combined frizzle dwarfs were greatly depressed by the moult in the second experiment, the merit of both genotypes for egg production, especially that of the single frizzle, should not be definitely rejected. The use of frizzle dwarfs could eventually be of interest for small-scale production if the moult could be avoided by means of an extra supply of light.

The current relation between the egg price and feed price in the egg market of Maputo (2.8) is considerably low, if compared with other neighbouring countries (4.3 in South Africa; 3.5 in Zimbabwe). The low ratio reflects the ceiling effect of imports on egg

price as well as the increased cost of imported feed ingredients, on which the local poultry industry depends. Such ratio imposes to the farmer the need for greater feed efficiency, on the one hand, and tighter control of the remaining allocated and overhead costs, on the other hand. In this regard, the higher contribution margin of the dwarf hens, which also reflects lowered production cost would be advantageous. Dwarf hens would also better withstand unexpected variations on the feed price to egg price ratio. As a matter of fact, in conditions similar to the present study, normal feathered and naked neck dwarfs would be 17 % less sensible to an increase in feed price and 7 % more resistant to a hypothetical decrease in egg price than the normal type of layer.

The distinction between margin per bird versus per area may change interpretation greatly. Considering a population density 30 % higher, the return on capital invested per unit of area allocated would potentially increase by as much as 50 % if dwarf instead of normal birds were used. Basing the analysis on a less conservative density (1.5 dwarfs *vs* 1 normal per unit of area) would increase the margin per area up to 70 %. The advantage of the dwarf layer-strain pullets for either large or small-scale production, however, lies beyond the farmers' monetary returns. In view of the scarcity of space in the households for backyard production and given the fact that major investments to expand the existing commercial sector are not expected, greater output per area could mean an increased supply of eggs in the market of Maputo. In the long run, increased local production at lowered production cost could to a certain extent hamper importation from external markets. In such conditions, the use of dwarf hens for egg production would be socially and economically meritorious.

6 CONCLUSION

The research has confirmed the hypothesis that the selected genes are not equally responsive to the environment. This is substantiated by different gene-environment interactions regarding growth, maturity rate, egg production, feed utilization, and survivability, reflecting varying biological and economic efficiencies.

The nutritional treatments introduced a varied response on egg weight (diet-*Na* and diet-environment interactions), but did not interfere with the dominant effects of climate on the remaining traits analysed.

Therefore, it can be deduced from the results that:

- None of the feathered-reduced genes (*Na* or *F*) could improve significantly the productive adaptability of the birds to the environmental conditions of the subtropical coastal region of South-East Africa.

- The normal feathered dwarf (*nana ff dw-*) is the most likely genotype to be used in peri-urban and rural egg production systems in Maputo, based on the higher feed conversion and lower production cost.

7 RECOMMENDATIONS

Given the prospects advocated in the introductory part of this work for developing egg production in the peri-urban and rural production systems of Maputo, the following recommendations could be derived from the present results:

- To consider the use of a dual purpose layer strain carrying the dwarf gene (*dw*) in future breeding policies and commercial exploitation in the southern region of Mozambique.

- To carry out further research in order to evaluate the productivity of layers carrying the naked neck gene (*Na*), either normal size or dwarf, in the more stressful tropical environments of the northern and central coastal regions of Mozambique.