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HAIR COAT CHARACTERISTICS IN FRIESIAN HEIFERS IN THE NETHERLANDS AND KENYA

EXPERIMENTAL DATA AND A REVIEW OF LITERATURE

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CONTENTS

1. INTRODUCTION

An agreement between the Netherlands and Kenya concerning the exportation of 5000 Dutch Friesian heifers to Kenya provided an opportunity of studying problems that arise when European cattle are exported to tropical countries. From 1971, 1000 heifers were to be delivered annually to the Kenyan Ministry of Agriculture. But this export scheme stopped in November 1973 after about 2600 heifers had been introduced into Kenya. Within the framework of the NUFFIC (Netherlands Universities Foundation for International Cooperation) a research project 'Adaptation of Dutch Friesian heifers in the Tropics, with special reference to Kenya' was set up to study adaptation problems. This project covered several subjects, e.g. health parameters, reproduction and growth. The present study, which deals with the hair coat, was part of the project.

Environmental conditions are mutable, and therefore the only passport to survival for an organism is adaptability (DE BEER, 1972). The hair coat is an aspect of environmental adaptation in certain mammals: it is the boundary between the animal and the surrounding physical environment and reflects the animal's response to that environment. Thus the coats of Scottish Highland cattle are admirably suited to withstand the harsh wintry weather this breed experiences, and they differ greatly for example from the coats of tropical Zebu cattle. But in addition, the coat of an individual animal changes in response to seasonal environmental changes. These seasonal variations in the hair coats of cattle are photoperiodically controlled (YEATES, 1954 and 1955). From this relationship it may be inferred that when European cattle are transferred from temperate climates to tropical areas, they will experience problems in adapting.

Workers in South Africa and Australia have stressed the importance of coat type in the successful adaptation of beef cattle to hot environments (BONSMA, 1949; TURNER and SCHLEGER, 1958, 1960 and 1970; SCHLEGER and TURNER, 1960; SCHLEGER, 1962; TURNER, 1962; BEILHARZ, 1972), and consequently the hair coat is regarded as a guide for judging the adaptability of beef cattle to tropical conditions. However, to our knowledge, until the present study no work has been done to ascertain what changes in the hair coat will occur in European dairy cattle in response to new conditions of photoperiodicity and prevailing climate.

This study is primarily concerned with the changes that occur in the hair coats of Friesian heifers that had been introduced into Kenya. A review of existing literature about the hair coat characteristics of cattle revealed that most studies had been made in Australia, on British beef and Zebu animals. Little work has so far been done on cattle in Europe. Therefore, to complement the Kenyan research project, we decided also to study hair coat changes in Friesian heifers kept under conditions prevailing in the Netherlands.

This report is divided into 2 main parts: a literature review and an account of our experiments.

The comprehensive review of literature (chapter 2) begins with basic facts about hair follicles, sweat glands and hairs, and then relates them to heat exchange, performance and adaptation. The resulting overview of current views on hair coats provides the background for our experiments.

Next the experiments are presented (chapter 3). Paragraph 3.1. describes the methods used; 3.2. the hair coat characteristics of the heifers in the Netherlands; and 3.3. the hair coat characteristics of the heifers imported to Kenya. In the discussion (chapter 4) the data from the experimental heifers in the Netherlands, from those taken to Kenya, and from the literature review are compared.

2. LITERATURE

2.1. ANATOMY AND PHYSIOLOGY OF THE HAIR FOLLICLE AND SWEAT GLAND

The skin of mammals is divided into an outer thin, cellular epidermis, and a connective tissue layer called the corium or dermis. The dermis contains hair follicles and glands, which are in fact epidermal structures produced as downgrowths from the epidermis.

The anatomy and physiology of hair follicles have been studied in relatively few species, mainly laboratory mice and rats, sheep, and man. Most studies have been carried out to gain a better understanding of some of the biological principles that regulate hair growth. In sheep the wool follicle is studied in its role as a production unit. In some domestic animals, notably cattle, the structural aspects of sweat glands and also of follicles have been studied, because of the important role that they play in thermoregulation.

2.1.1. *Hair follicle and hair fibre*

Hair follicles and sweat glands are developed as downgrowths from the epidermis (LYNE and HEIDEMAN, 1959; MONTAGNA and VAN SCOTT, 1958). In cattle the initiation of hair follicles begins at about the 77–78th day of foetal life (LYNE and HEIDEMAN, 1959 and 1960). Follicle initiation ceases at about the 166th day of foetal life in *Bos taurus* (LYNE and HEIDEMAN, 1959) and at about the 180th day of foetal life in *Bos taurus* × *Bos indicus* crosses (LYNE and HEIDEMAN, 1960). So the total follicle number of an animal is determined at the time it is born. In cattle every follicle is associated with a sweat gland (LYNE and HEIDEMAN, 1959), a sebaceous gland and an erector pili muscle.

In sheep there are two kinds of follicles: primary follicles which are formed first, and secondary follicles which are formed later in clusters associated with the primaries (RYDER, 1973). Secondary follicles form only a sebaceous gland, and do not develop either a sweat gland or an erector pili muscle (RYDER, 1973).

After the follicle has developed fully, hair fibre growth occurs in cycles in which periods of growth alternate with periods when the follicle is quiescent.

Figure 1 shows an active hair follicle. The wall of the follicle forms an inner and outer root sheath for the hair (RYDER, 1973). In the centre of the follicle is the hair. The concentric parts of the hair: cuticle, cortex, and medulla, as well as the inner root sheath, originate as separate streams of cells in the follicle bulb (MONTAGNA and VAN SCOTT, 1958). Inside the bulb is the papilla.

2.1.1.1. Bulb and papilla

The bulb of the hair follicle (Figure 2) can be divided into a lower region of undifferentiated cells (the pre-elongation region) and an upper region (the elongation region) in which the cells become differentiated to form the inner root sheath and the hair. A line across the widest part of the papilla would

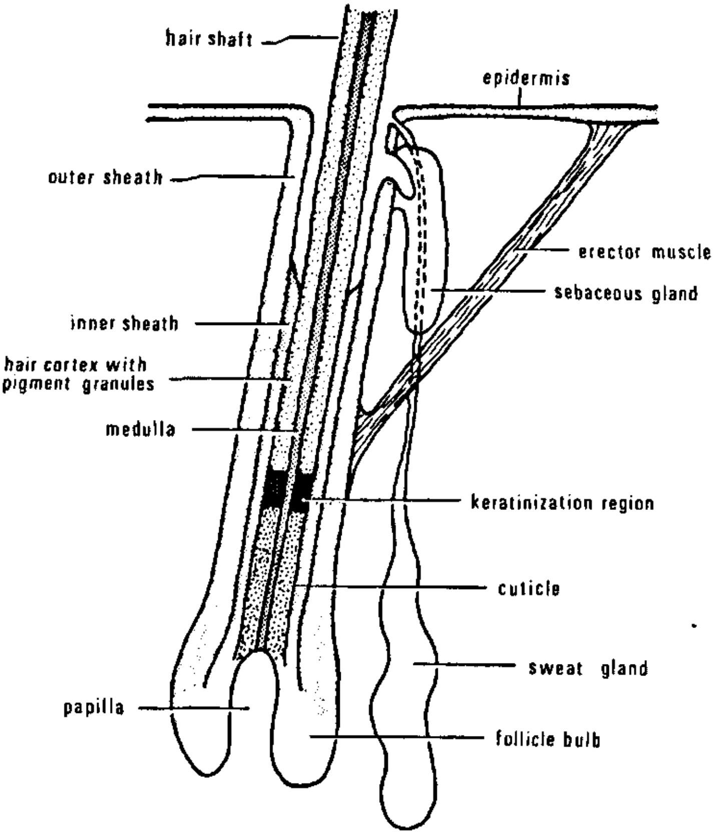


FIG. 1. Active hair follicle (after RYDER, 1973).

separate the two regions at the critical level (AUBER, 1952). Below the critical level is the matrix, or germination centre of the follicle (AUBER, 1952; FRASER, 1965; MONTAGNA and VAN SCOTT, 1958). EPSTEIN and MAIBACH (1967) have also found matrix cells above the critical level close to the papilla.

The cells of the matrix of an active hair follicle possess a high potential for mitotic activity (MATOLTSY, 1958; PARAKKAL, 1967). They divide, move up in orderly rows, and differentiate into the hair and the inner root sheath (EPSTEIN and MAIBACH, 1967; MONTAGNA and VAN SCOTT, 1958). The outer root sheath is self-propagating (MONTAGNA and VAN SCOTT, 1958). When the newly produced cells ascend to the level of the pre-elongation region of the bulb, they are still capable of dividing. Near the neck of the bulb, in the elongation region, the nuclei of these cells change from a round to an oval form and the cells increase in volume. As the cells pass through the neck of the bulb and reach the pre-keratinization region they become still larger and become elongated (MATOLTSY, 1958).

Inside the bulb is an egg-shaped cavity, the papilla, that is completely filled with loose connective tissue (MONTAGNA and VAN SCOTT, 1958).

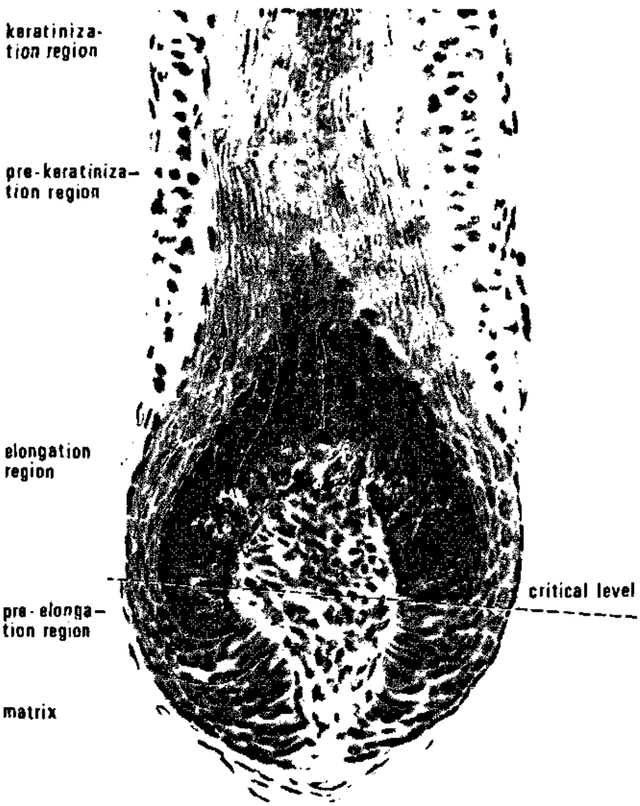


FIG. 2. Longitudinal section through the bulb of a hair follicle.

2.1.1.2. The hair fibre

The matrix cells give rise to three or four types of cells: those of the hair cuticle, the hair cortex, the hair medulla (which is sometimes absent), and the inner root sheath.

Hairs have a thick cortex, a one-layered outer cuticle and sometimes a central medulla. The cortex is composed of fusiform, keratinized cells cemented together; single cortical cells cannot be distinguished in it (MONTAGNA and VAN SCOTT, 1958; MATOLTSY, 1958). Whether or not a medulla will be formed seems to depend on the papilla dimensions (HENDERSON, 1965). The matrix cells closest to the papilla give rise to the medulla (PARAKKAL, 1967). The main feature of medulla formation is the vacuolation, which begins in the interstices between the cells (MONTAGNA and VAN SCOTT, 1958; PARAKKAL, 1967). PARAKKAL studied the active hair follicle of the mouse: he found that during differentiation the cortical cells immediately adjacent to the medullary cells progressively project into them, so that sometimes opposite cortical cells may meet each other and make the medulla discontinuous.

The cells of the hair cuticle, being flat, are known as scales; they overlap like the tiles on a roof (MONTAGNA and VAN SCOTT, 1958; RYDER and STEPHENSON, 1968). The minimum number of scales needed to encircle a hair is two; even in the fine fibres of sheep a cuticular scale is never tubular (RYDER, 1973).

The cells of the cuticle of the hair interlock with those of the inner root sheath, firmly anchoring the hair in the follicle (MONTAGNA and VAN SCOTT, 1958).

Basically there is no difference in fibre structure between different species. In sheep, three main kinds of fibre are recognized: wool fibres, hair fibres, and kemp fibres (Figure 3). In domestic sheep these three types of fibre are generally called 'wool' (RYDER and STEPHENSON, 1968). Kemp fibres are very coarse; their main feature is the wide latticed medulla occupying most of the width of the fibre. Kemp fibres grow only in primary follicles. Secondary follicles grow wool fibres. Fine wool is usually tightly crimped and lacks a medulla (RYDER and STEPHENSON, 1968). Coarse wool fibres have a small medulla. Hairs grow mainly in primary follicles, they are intermediate in diameter between wool and kemp fibres, have a medulla in the wide part of the fibre grown in summer, but are non-medullated in the narrow part grown in winter (RYDER, 1973).

All cattle follicles are homologous with the primary follicles of sheep. In the literature, the fibres growing in the follicles of cattle are referred to as hairs. They vary widely, from kemp-like fibres with a wide medulla to non-medullated fibres resembling wool.

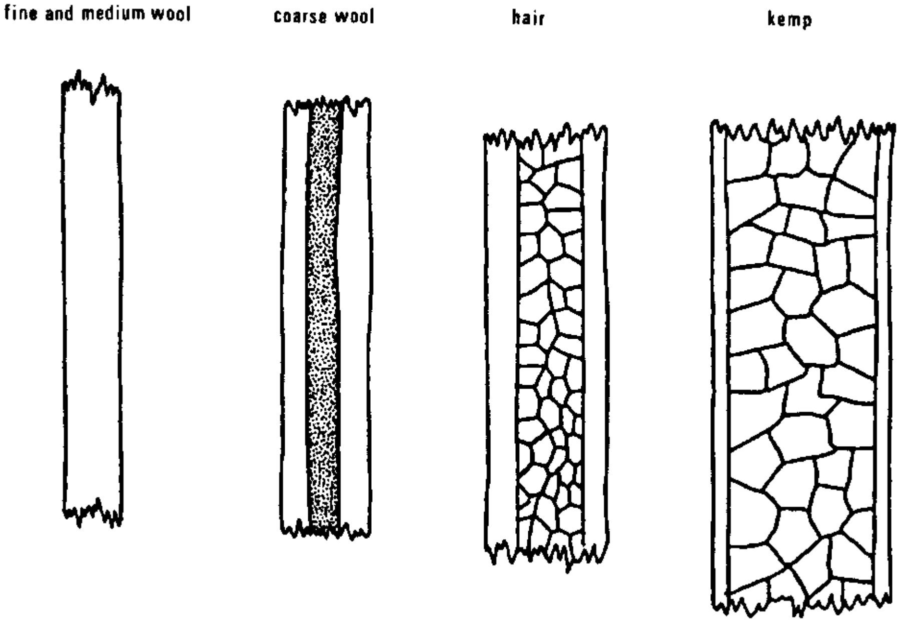


FIG. 3. Sections of the main fibre types in sheep (after RYDER, 1973).

In the following pages wool is used especially for fibres grown in secondary follicles and hair is used for fibres grown in primary follicles or in follicles homologous with primary follicles.

2.1.1.3. Relation of follicle structure to hair fibre

BURNS and CLARKSON (1949) measured various dimensions on only a small number of wool follicles and found that the cross-sectional area of the fibre was highly correlated with the volume of the follicle bulb and papilla. HENDERSON (1965) measured the wool follicle and fibre dimensions of a number of Romney sheep and concluded that differences in fibre diameter from individual follicles within one follicle population result from differences in the amount of germinative tissue within the follicle bulb.

HENDERSON (1965) and STRAILE (1965) found that medulla-producing follicles had much larger bulbs and papillae compared with follicles producing wool fibres, and their papilla occupied a larger proportion of their bulb volumes.

HENDERSON (1965) also found a positive correlation between follicle and fibre length. According to him and to SLEE and RYDER (1967), change in fibre length depends on the number of cell divisions in the bulb.

NAY and JOHNSON (1967) found a correlation coefficient of $r = 0.84$ between the hair follicle diameter and hair fibre diameter in British Friesian bulls.

2.1.1.4. Blood supply of the follicle

Various workers (e.g. DURWARD and RUDALL, 1958; BULLOUGH and LAURENCE, 1958; RYDER, 1958) mention the importance of an excellent blood supply for active hair growth. The growing fibre is fed by blood vessels around the outer surface of the lower third of the follicle and in the papilla (DURWARD and RUDALL, 1958). The larger the papilla the more vessels it contains (DURWARD and RUDALL, 1958; RYDER, 1958). According to RYDER (1958), a large follicle has an extensive blood supply because it is large, and it is not the extensive blood supply that makes it large.

The vessels of the papilla supply substances needed for cell division.

The function of the basket-like network of capillary vessels surrounding the lower third of the follicle is less clear. These vessels do not extend above the point at which the fibre becomes keratinized, which suggests that they could provide substances needed in the keratinization process (RYDER and STEPHENSON, 1968).

2.1.1.5. Hair keratinization

The transformation of living epithelial cells into horny structures, such as hair, is called keratinization (MATOLTSY, 1958; YOSHIMURA, 1964). The hair keratinizes about one-third of the way up the follicle (Figures 1 and 2). At least 4 different cell layers (those of the medulla, cortex, cuticle and inner root sheath) are involved (PARAKKAL, 1967). The cells reach their maximum size in the keratogenous zone (Figure 2). Keratinization involves the transformation of cytoplasmic protein in these cells into keratin fibres, the disintegration of the keratinizing cells, and the decomposition of the cytoplasm and nucleus (YOSHIMURA, 1964).

The main chemical change that occurs in the fibre during keratinization is the oxidation of two sulphydril (SH) groups to form one disulphide (S-S) link (YOSHIMURA, 1964; MATOLTSY, 1958). By this cross linkage the protein is stabilized and becomes resistant to enzymatic as well as to chemical hydrolysis (YOSHIMURA, 1964; MERCER, 1967; MATOLTSY, 1958).

Medullary cells do not keratinize in the same way as the cortical cells. The medulla cells contain about 95% keratin, whereas the mature cortical cells are filled almost entirely with keratin (MATOLTSY, 1958).

2.1.1.6. Hair pigmentation

Hair fibre colour is chiefly determined by the amount of the pigment melanin that is present (MEYER, 1962; RUSSELL, 1939; LEA, 1954; SCHLEGER, 1962). Melanin occurs in granules that are found (according to MEYER (1962) and RYDER (1973)) in the cuticle, cortex, and medulla of the fibre; the inner root sheath remains non-pigmented. According to MONTAGNA (1958) the cuticle also remains non-pigmented. Melanin granules are produced by pigment-forming cells known as melanocytes (FITZPATRICK et al., 1958; BARNICOT and BIRBECK, 1958; YOSHIMURA, 1964; MOTTAZ and ZELICKSON, 1967).

Skin pigmentation is due to the activity of the melanocytes located in the basal layer of the epidermis; pigmentation of the hair fibres is due to activity of the melanocytes located in the upper part of the bulb (MONTAGNA, 1958; FITZPATRICK et al., 1958). There are two kinds of melanin: eumelanin, which gives brown-black coloration; and phaemelanin, which gives the yellow-red coloration. Both appear to be formed by initial oxidation of tyrosine with the copper-protein enzyme tyrosinase. A complicated series of oxidations and polymerizations of intermediate products leads to the final formation of melanin (MOTTAZ and ZELICKSON, 1967; FITZPATRICK et al., 1958; DANIELS, 1964; RUSSELL, 1939; YOSHIMURA, 1964). The exact chemical structure of melanin has yet to be established.

Variations in the amount of melanin under various physiological circumstances are related to differences in melanocyte activity rather than to the number of melanocytes (YOSHIMURA, 1964; BREATHNACH, 1971).

There is evidence that pigment production is hormonally controlled. According to BREATHNACH (1971), pituitary, adrenal, gonadal, and thyroid hormones all have some influence upon pigmentation, but it is unclear how they act. BERMAN (1960) states that the melanocyte-stimulating hormone of the pituitary controls melanin dispersion within the melanocytes, but does not affect pigment synthesis. According to RYDER (1973) the melanocyte-stimulating hormone is inhibited by the hormones of the adrenal cortex. In cattle local application of thyroxine has been found to increase the pigmentation (BERMAN, 1960).

2.1.2. *The sweat gland*

There are two kinds of sweat glands: eccrine and apocrine. The eccrine glands are smaller than apocrine glands, and secrete a dilute salt solution (Yoshimura, 1964). Apocrine sweat glands secrete a fluid containing fatty materials and lose part of the cellular protoplasmic substance when functioning.

The structure and function of sweat glands vary greatly between species.

The sweat glands of cattle (like most mammals) are generally regarded as apocrine in type (Findlay and Yang, 1950; Dowling, 1955; Hafez et al., 1955; Nay and Hayman, 1956). They are sac-like structures, lying at the base of each hair follicle and with a narrow duct opening into the follicle (Figure 1) (Findlay and Yang, 1950; Yeates, 1965; Carter and Dowling, 1954). Nay (1959) recognized three different gland shapes in cattle (Figure 4): the tubular more or less coiled type (a, b, c, d); the baggy type with wide diameter (i, j); and the club-shaped, intermediate type (e, f, g, h).

Sweat glands are composed of two layers of cells; an outer myoepithelium and inner glandular epithelium (Findlay and Yang, 1950). The glands have a poor blood supply (Goodall and Yang, 1952).

For a long time it was not known whether or not cattle sweat. For instance, in 1950 Findlay and Yang concluded that sweating in Ayrshire cattle was unimportant as a source of heat loss. Ferguson and Dowling (1955), Dowling (1955), McDowell et al. (1955), and Taneja (1959c) were the first to show that a sweating mechanism is important in cattle.

Once sweating is initiated in the cow it continues at a very uniform rate

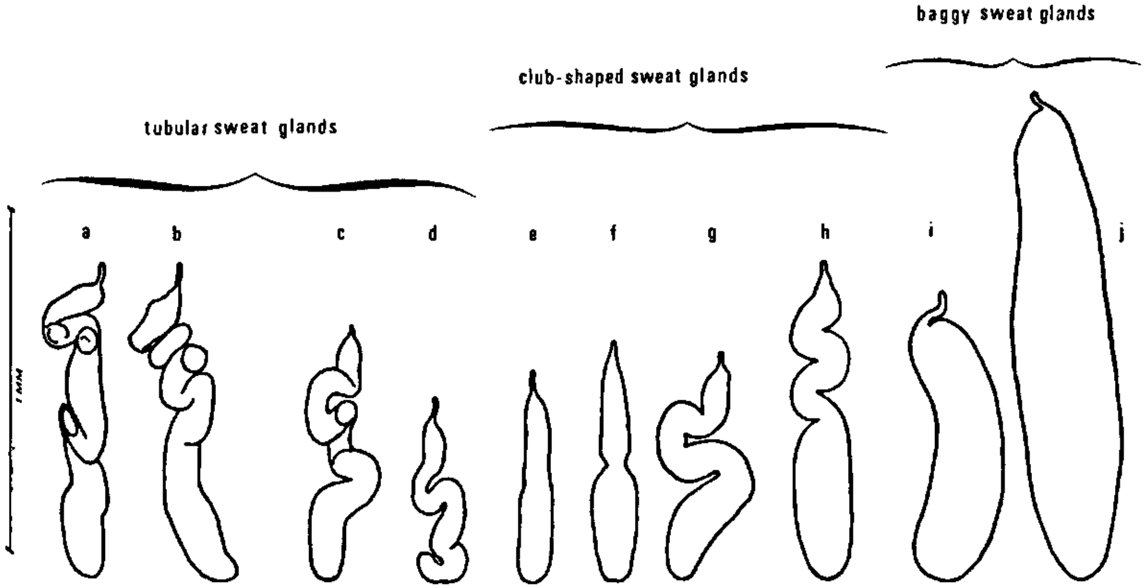


Fig. 4. Various types of sweat glands in cattle (after Nay, 1959).

(McDowell et al., 1961); this is contrary to the theory of the mode of action by apocrine type glands.

The mode of secretion is still unclear. It appears to be controlled by an adrenergic mechanism (Ferguson and Dowling, 1955; Taneja, 1959b; Findlay and Robertshaw, 1965; McDowell et al., 1961), requiring intact sympathetic nerves. Yet there are no nerves supplying the sweat glands (Findlay and Robertshaw, 1964). Yeates (1965) has suggested that adrenalin activates the muscle fibrils of the sweat glands, which presumably leads to the ejection of sweat. The glands are always full of a fluid-like (colloidal) material, and the glandular epithelium appears to be intact during the secretion process (Findlay and Jenkinson, 1960). So, according to Findlay and Jenkinson, the moisture loss from these glands must either be by diffusion into the lumen and hence to the skin surface, or by a process of secretion that does not involve degeneration of the glandular epithelium.

Alvarez et al. (1970) have proposed a so-called 'blood-flow interstitial fluid theory' as a possible explanation for cutaneous moisture loss in cattle. In a hot environment there is an increased flow of blood to the skin, which increases the water supply to the sweat gland and the volume of interstitial fluid in the epidermis. The accumulation of fluid around the epithelial cells of the sweat gland would create a difference in hydrostatic pressure and water would therefore flow from the higher pressure area to the lower pressure area (lumen of the gland). According to Alvarez et al. these conditions cause more water to be lost by diffusion through the sweat gland.

2.1.3. *Growth cycle of the follicle*

Hair growth is an intermittent process; the hair passes from active growth (anagen) through an intermediate phase (catagen) to a resting stage (telogen) and then back to anagen (Roth, 1965; Chase, 1965; Johnson, 1965; Van Scott et al., 1957; Van Scott, 1965).

2.1.3.1. Anagen

When a quiescent follicle becomes active again, the basal cells of the lower follicle grow downwards as a solid column of undifferentiated and dividing cells to surround the papilla (Bullough and Laurence, 1958; Montagna and Ellis, 1958).

In a fully grown and fully active follicle (Figure 2) the only mitotic activity is that of the matrix (Van Scott, 1965; Bullough and Laurence, 1958).

The high mitotic activity of a hair bulb can only be maintained by a high level of energy production in the cells (Bullough and Laurence, 1958).

In the anagen stage, tyrosinase activity and hair pigmentation is at maximum (Fitzpatrick et al., 1958; Schleger and Bean, 1973).

Schleger (1966) and Schleger and Bean (1971) have shown that the size of the sweat glands in cattle varies with each phase of the hair growth cycle.

The capillary supply to sweat glands is derived mainly from the capillary plexus of the keratogenous zone of active follicles (Schleger and Bean, 1971).

So the growth phase of the follicle appears to have a critical effect on the capillary supply to the sweat gland.

2.1.3.2. Catagen

Catagen is the short transition stage between active growth and the resting stage (Figure 5). Pigment ceases to be delivered to the cells of the hair, mitotic activity in the matrix stops, the bulb ceases to exist as such, the follicle shortens to about half its length, and the last differentiated keratinized cells are incorporated into a club shaped mass, also called the brush-end (CHASE, 1965; MONTAGNA and VAN SCOTT, 1958).

The papilla is free but remains touching the epidermal strand (MONTAGNA

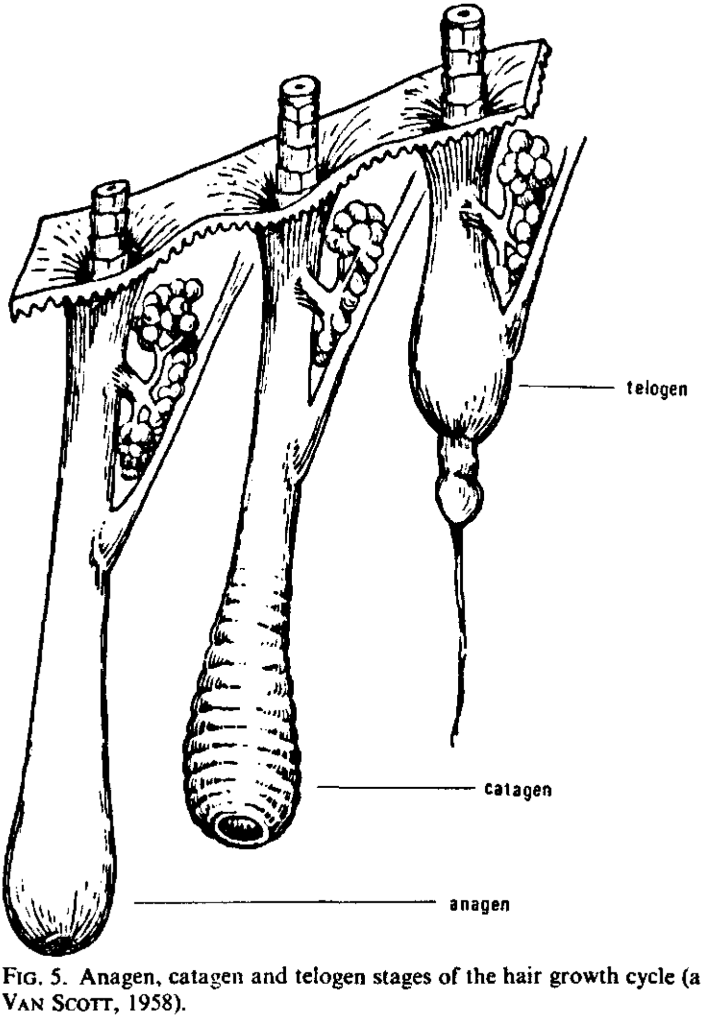


FIG. 5. Anagen, catagen and telogen stages of the hair growth cycle (after MONTAGNA and VAN SCOTT, 1958).

and VAN SCOTT, 1958), and the number of blood vessels near the bulb decreases (CHASE, 1965).

2.1.3.3. Telogen

When catagen is complete the follicle enters the resting or telogen stage. The follicle is now completely inactive. Neither inner nor outer root sheath are present (this distinguishes the telogen stage from the catagen stage), and the club is surrounded by an epithelial sac (CHASE, 1965; VAN SCOTT, 1965). The papilla persists in telogen only as a ball of cells, often out of morphological contact with the follicle (COHEN, 1967). Figure 5 depicts a resting follicle.

In the telogen stage the melanocytes become dormant (CHASE, 1965; FITZPATRICK et al., 1958), and according to MONTAGNA (1958) there is no enzyme activity during this stage.

According to SCHLEGER (1966) and SCHLEGER and BEAN (1971), in cattle the sweat gland undergoes cyclic changes in morphology in association with the hair follicle. In 1966 Schleger stated that the sweat gland is completely regressed in telogen, but in 1971 SCHLEGER and BEAN reported that in new studies they never found complete regression of the sweat gland in telogen. Contrary to the findings of SCHLEGER and of SCHLEGER and BEAN, JENKINSON and NAY (1968) observed full-sized sweat glands in all stages of the hair cycle.

2.1.3.4. Regulation of growth cycle of the follicle

There are three main types of hair growth cycles: seasonal, wave and mosaic. In seasonal cycles (e.g. in cats, dogs, horses, deer, cattle and wild sheep) the hair is shed either once or twice a year. Hair growth waves occur in the fur-bearing rodents: in these animals waves of activity pass over the body in definite patterns. In man and in the guinea pig the growth pattern is a mosaic one; in this type the hairs are replaced irregularly (VAN SCOTT et al., 1957; RYDER, 1973).

The way in which the follicular cycle is controlled is still not understood (JOHNSON, 1965). The initiation of growth in a follicle is probably accompanied by an engorgement of capillaries (JOHNSON, 1965; RYDER, 1958), and is not a response to increased vascularity, as was suggested by DURWARD and RUDALL (1949).

CHASE (1955) suggested that the follicular rhythm depends upon the accumulation of an inhibitor during active growth and its dispersal during the resting stage. In the long cycles of sheep and man this hardly seems possible. JOHNSON (1965) has tested CHASE's suggestion by plucking hairs from rats at different stages of the hair cycle. If the follicular rhythm were controlled by the build up of an inhibitor during active growth it might be expected that after a hair had been plucked there would have been a period of growth lasting as long as the normal period of growth. If an inhibitor were removed by plucking during the resting stage, activity should have been induced after a constant interval. JOHNSON found that the plucking of growing hairs in fact shortened the period of activity, and that follicular activity was advanced by plucking at the beginning of the resting period, unaffected by plucking at 12 days before expected eruption, and delayed by plucking between 12 and 7 days before expected eruption. Her results are more easily explained by supposing that the follicular rhythm depends upon an inductive stimulus, rather than by accepting the hypothesis of accumulation and dispersal of an inhibitor.

This stimulus is, according to BULLOUGH (1962), not nervous, and is not caused by the diffusion of some substance from follicle to follicle.

HOUSSAY (1962) suggested that the hair waves are regulated by a balance between stimulating and inhibitory factors. And according to HOUSSAY et al. (1965) these stimulants and inhibitors may be hormones.

2.1.3.5. Hormonal control of the growth cycle of the follicle

Most of the information about hormonal influences upon hair growth cycles comes from observations in laboratory mice and rats. In these animals, spontaneous growth begins periodically in the belly and spreads dorsally as a wave (MONTAGNA, 1958). In sheep, the effect of hormones on the rate of hair growth has been studied.

When comparing the reactions of the follicles of mice and rats with wool fibre follicles, there is a need for cautious interpretation. In the cyclical hair follicle there is intense mitotic activity (2–3 weeks) followed by longer periods of quiescence, whereas in most domestic sheep the wool follicle has a very long growing period.

There seem to be at least four endocrine glands that influence hair growth by the hormones they secrete into the bloodstream. These are the pituitary, the thyroid, the adrenal cortex, and the gonads.

The pituitary gland

Hypofysectomy accelerates the initiation of spontaneous hair growth waves in mice and rats (MOHN, 1958; HOUSSAY et al., 1965). According to MOHN and HOUSSAY et al., the principal action of the pituitary gland on the hair cycle is an inhibitory one through its influence upon the gonads and adrenals, although it probably stimulates hair growth through the thyroid gland (MOHN, 1958). The growth hormone has no effect on hair growth but affects the quality of the pelage (MOHN, 1958).

Removal of the pituitary gland in sheep causes wool growth to drop to a very low level (FERGUSON et al., 1965; RYDER and STEPHENSON, 1968). FERGUSON et al. (1965) found that an unidentified pituitary factor, free of thyrotrophic activity, stimulated wool growth in hypofysectomized sheep.

The thyroid gland

The resting phase of hair growth in rats and mice can be lengthened by suppressing thyroid secretion, either by thyroidectomy or by the administration of anti-thyroid agents (MOHN, 1958; EBLING, 1965; HOUSSAY et al., 1965). However, suppression of thyroid secretion has no effect on follicles already in anagen (MOHN, 1958). The administration of thyroid hormones restores hair growth waves in thyroidectomyzed or prophylthiouracil-treated animals.

In sheep, thyroidectomy decreases wool growth (ROUGEOT, 1965; FERGUSON et al., 1965; RYDER and STEPHENSON, 1968). A similar effect is produced by administering anti-thyroid agents (ROUGEOT, 1965). Administration of thyroxine to sheep with an intact thyroid stimulates wool growth (RYDER and STEPHENSON, 1968). ROUGEOT (1965) established that the length of the fibres varied greatly depending on the circulating level of thyroid hormones, without a change in fibre diameter.

BERMAN (1960) *found that the local application of l-thyroxine increased* hair growth by 18% in cattle.

These findings suggest that thyroid hormones have a physiologically stimulating effect on hair growth. FERGUSON (1958) postulated that the stimulating effect of thyroxine on wool growth is due to general increase in metabolic rate following its administration. DOWNES and WALLACE (1965) studied the local effect of thyroxine on wool growth is due to a general increase in metabolic rate creased the length of the fibres. Their results suggest that thyroxine may directly affect the output of follicles, apart from indirectly causing changes in appetite or in general metabolism. BERMAN (1960) injected l-thyroxine intradermally in cattle; he also concluded that thyroxine has a direct effect on hair growth.

The adrenal cortex and gonads

Adrenalectomy and gonadectomy induce quiescent follicles to become active in rats and mice (MOHN, 1958; EBLING, 1965; HOUSSAY et al., 1965). Delay in the onset of activity is brought about by estrogen, testosteron, and ACTH (MOHN, 1958; EBLING, 1965). Daily treatment with small doses of cortisone inhibits the spontaneous initiation of hair growth in intact, gonadectomized or adrenalectomized rats, but has no effect on the follicles already in anagen (MOHN, 1958). The adrenal cortex restrains the initiation of spontaneous growth by means of its glucocorticoids.

LINDNER and FERGUSON (1956) and DOWNES and WALLACE (1965) found that adrenal cortex hormones depress the rate of wool growth.

In cattle the application of a synthetic adrenal corticoid analogue to the skin was found to depress the initiation of new hairs (TURNER and SCHLEGER, 1970).

2.1.4. *Summary*

Most studies about hair follicles referred to in this chapter have been made on laboratory animals, sheep, and man. There is a great uniformity in results between different species.

In cattle the total follicle number of an animal is fixed at birth. All follicles in cattle are homologous with the primary follicles of sheep; each follicle is associated with a sweat gland, as well as a sebaceous gland and an erector pili muscle.

Fibre dimensions are controlled by the size and shape of the bulb and papilla (the lowest parts of the follicle). Medullated fibres have much larger bulbs and papillae compared with follicles producing non-medullated fibres.

Unlike the hair follicle, the structure and function of the sweat gland vary strongly among species. Little agreement exists between authors on the mode of secretion of sweat glands.

Hair colour is chiefly determined by the amount of the pigment melanin that is present.

Hair fibre growth occurs in cycles in which periods of growth alternate with periods when the follicle is at rest.

According to SCHLEGER (1966) and SCHLEGER and BEAN (1971) the sweat gland in cattle undergoes cyclic changes in morphology in association with the hair follicle. JENKINSON and NAY (1968) however, observed full-sized sweat glands in all stages of the hair growth cycle.

In the growth stage, hair pigmentation is at its maximum.

The way the follicular cycle is controlled remains a fundamental problem of hair growth. Experiments with laboratory rats and mice generally indicate that the thyroid appears to provide a hormonal pathway for acceleration and

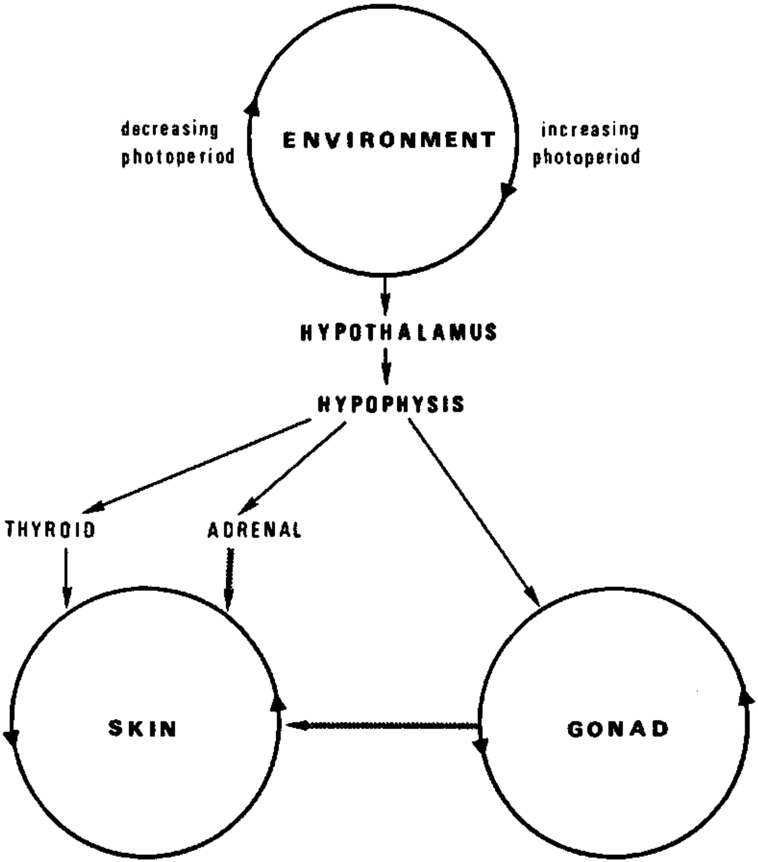


FIG. 6. Schematic representation of relationship between environmental, gonadal and skin cycles (after EBLING, 1965). Unbroken lines represent pathways of acceleration; broken lines pathways of inhibition.

the adrenal cortex and gonads pathways for retardation of the hair growth waves. Once the wave has commenced, few hormones have effect. In contrast, in sheep the hormones do affect the rate of growth.

In cattle thyroxine has been found to stimulate hair growth whereas adrenal corticoids depressed the initiation of new hairs. It is known that hormones regulate but do not create processes. The actual mechanism of the regulation of the hair growth waves in laboratory animals is still not understood. In a number of species, coat shedding is influenced by seasonal change in length of day (this is discussed later in paragraph 2.4.).

According to EBLING (1965), the hormonal pathways that influence hair growth and the relationship between shedding and changes in photoperiod in animals that have a seasonal hair growth cycle suggest that these seasonal cycles are linked to the same light cycle that controls the breeding season through the eyes and the anterior pituitary gland (Figure 6). However, according to RYDER and STEPHENSON (1968) this approach is probably an oversimplification.

2.2. HAIR FOLLICLE AND SWEAT GLAND CHARACTERISTICS IN CATTLE

Investigations on hair follicle and sweat gland characteristics have been carried out in cattle,

- to provide a morphological basis for comparisons between different breeds in different habitats (JENKINSON and NAY, 1972 and 1973)
- to determine evolutionary trends in sweat gland development (NAY, 1959)
- to investigate the functions of the sweat glands of cattle
- to determine whether skin type could be of value in the selection of cattle for tolerance to different environments (JENKINSON and NAY, 1972).

2.2.1. *Sampling*

FINDLAY and YANG (1950) and HAFEZ et al. (1955) obtained skin samples by cutting pieces of skin from hides. This method does not permit continuous study of individual living animals under experimental conditions nor the observation of sufficiently large test groups. Detailed studies have been facilitated by the use of a biopsy punch.

CARTER and DOWLING (1954) obtained skin samples by biopsy, using a 1 cm trephine under local anaesthesia. The trephine cuts a circle in the skin, which is then dissected away from its underlying fascia. This trephine biopsy technique has been used by various workers on hair follicle and sweat gland characteristics (e.g. DOWLING, 1955; NAY and HAYMAN, 1956; HAYMAN and NAY, 1958; DOWLING, 1964; TANEJA, 1960; TURNER, NAY and FRENCH, 1962; PAN, 1963; NAY and JOHNSON, 1967; SCHLEGER, 1966; PAN et al., 1969; ALLEN et al., 1963; JENKINSON and NAY, 1968, 1972 and 1973; SCHLEGER and BEAN, 1971 and 1973).

FINDLAY and JENKINSON (1960) also took biopsy specimens without using a local anaesthetic; they used an electric drill with a hollow-ended steel bit of internal diameter 0.37 cm. This high-speed punch technique has been applied by, among others, JENKINSON and NAY (1968, 1972) and JENKINSON et al. (1975).

Skin samples are mostly taken from the so-called midside area of an animal; an area between approximately the 10th rib and the hip bone, at a level approximately two-fifths of the distance from the thoracic vertebrae and lumbar vertebrae, and the belly.

Skin biopsy specimens are usually prepared for examination according to a method described by NAY and HAYMAN (1956) or to modifications of this method. Briefly these methods involve

- fixing in formol-saline
- cutting sections with a safety-razor blade or with a sledge microtome using a freezing stage
- staining the sections
- mounting the sections.

2.2.2. *Some hair follicle and sweat gland characteristics*

BONSMA (1949) distinguishes two kinds of follicles in cattle, in analogy with sheep; primary ones and secondary ones. But later workers (e.g. FINDLAY and YANG, 1950; CARTER and DOWLING, 1954; DOWLING, 1955; LYNE and HEIDEMAN, 1959) found that each hair follicle was associated with a sweat gland as well as a sebaceous gland and an erector pili muscle. So all hair follicles are homologous with the primary follicles of sheep.

HAYMAN and NAY (1961) found that approximately 6% of the follicles were much larger than the rest. These giant follicles lay at different angles to the surface, penetrated to a greater depth in the dermis, had a greater diameter, and were associated with a multilobular sebaceous gland and a much larger sweat gland than the other follicles.

In studies on hair follicle and sweat gland dimensions, follicles in the telogen stage and giant follicles are not measured.

2.2.2.1. Hair follicle length, hair follicle diameter, hair follicle depth, and angle of slope of the hair

Appendix 1 gives data from literature on hair follicle length, hair follicle diameter and hair follicle depth.

The hair follicle length (FL) is defined as the distance between the base of the bulb of an active hair follicle and the point where the follicle reaches the surface of the skin (Figure 7) (JENKINSON and NAY, 1968). Mean values for hair follicle length range from 1.5 mm in Jersey cows in Great Britain and in 471 animals of 42 breeds in Asia, to 2.0 mm in 1363 animals of 78 breeds in Europe (Appendix 1).

The diameter of follicles (FDM) (shortest distance between two opposite walls of the hair canal) is measured at the level of the sebaceous glands (Figure 7) (JENKINSON and NAY, 1968). Mean values range from 31 μ in Galloway cattle in Great Britain to 55 μ in 4 American breed groups (Appendix 1).

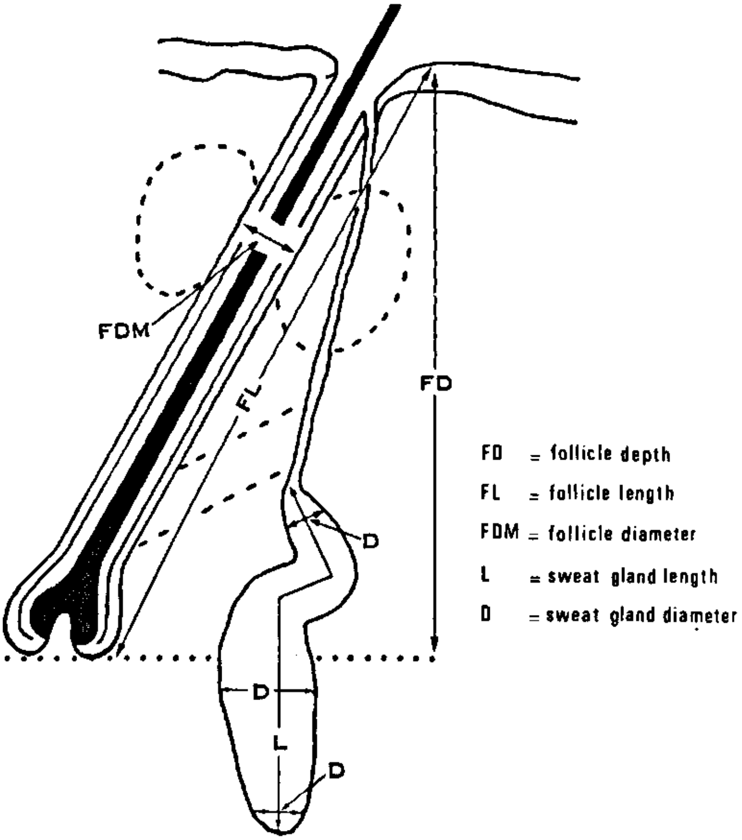


FIG. 7. Diagram illustrating the measurements made on skin sections (after NAY and JENKINSON, 1968).

The hair follicle depth (FD) is defined by JENKINSON and NAY (1968) as the shortest distance between the base of an active hair follicle and the skin surface (Figure 7). Mean values range from 0.8 mm in Muturu cattle in Nigeria to 1.9 mm in Galloway cattle in New South Wales, Australia (Appendix 1).

JENKINSON and NAY (1972 and 1973) calculated the angle of slope of the hair in different European, Asian, African, and American breed groups; mean values were respectively 61°39, 59°19, 58°41 and 60°13. In Great Britain in Friesian and Ayrshire cattle the angle of slope varied between 49° and 61° (JENKINSON et al., 1975).

2.2.2.2. The length, diameter, shape and volume of the sweat gland

Appendix 1 gives data found in literature about the length, diameter, shape and volume of sweat glands.

NAY and JENKINSON (1964) defined the sweat gland length (L) as the length of the secretory portion of the gland (Figure 7). The length of sweat glands is very variable, from 450 μ in Jersey cows in New South Wales to 1150 μ in Friesian bulls in Great Britain (Appendix 1).

In the literature the sweat gland diameter (D) is estimated by measuring the diameter of the secretory portion of each gland in three places (Figure 7). The estimates of sweat gland diameter range from 74 μ in Friesian cattle in Great Britain to 173 μ in Sindhi and Sahiwal cows in New South Wales (Appendix 1).

From the estimates of sweat gland length (L) and sweat gland diameter (D) the sweat gland shape, expressed as L/D is calculated. The L/D ratio ranges from 5.8 in Friesian cattle in Great Britain to 10.8 in 186 animals of 9 breeds in South America (Appendix 1).

The sweat gland shape is a measure of the extent to which animals tend to have simple sac-like structures or tubular glands (JENKINSON and NAY, 1968). In long, thin and convoluted glands the L/D ratio is much larger than in sweat glands of a simple shape (Figure 4).

By considering the sweat glands as cylindrical vessels the glandular volume is estimated using the formula $\pi\ (D/2)^2L$, in which D = diameter of the sweat gland and L = length of the sweat gland.

Appendix 1 shows that the range of volume is very wide varying from $4.2\ \mu^3 \times 10^6$ in Shorthorns in Queensland to $30.5\ \mu^3 \times 10^6$ in Sahiwals in New South Wales.

2.2.2.3. Hair follicle and sweat gland density

In cattle the number of hair follicles always equals the number of sweat glands. Therefore the hair follicle and sweat gland density per unit area of skin can be estimated by counting the follicles per unit area of skin.

CARTER and DOWLING (1954) showed that in estimating the population density of hair follicles or sweat glands a correction factor is needed to adjust for the shrinkage of the skin specimen. This correction factor is made by using a biopsy punch of known and accurate dimensions; the factor is obtained from the ratio: estimated area of the mounted section/internal area of the biopsy punch.

Data found in literature on hair follicle and sweat gland density are shown in Appendix 2. Mean values range from 650/cm^2 in Shorthorns in New South Wales (DOWLING, 1955) to as high as 3600/cm^2 in bulls in Egypt (HAFEZ et al., 1955).

The data from HAFEZ et al. (1955) and FINDLAY and YANG (1950) are not corrected for skin shrinkage. Later workers made corrections for the shrinkage of the skin specimen. According to CARTER and DOWLING (1954) the value of the correction factor may vary according to the age and body condition of the animals sampled. In their work they found that the correction factor was in the order of 0.45 for mature cattle. If the mean values of FINDLAY and YANG (1950) and of HAFEZ et al. (1955) are multiplied by 0.45 they are within the general order of densities mentioned in Appendix 2.

2.2.2.4. Skin thickness

In mature cattle in Queensland, skin thickness measurements were found to range from 5.8 to 6.8 mm in Shorthorn and Australian Illawara Shorthorns (AIS) cattle, and from 6.9 to 7.6 mm in Brahman × Shorthorn crosses (DOWLING, 1964). In 10 breed groups in Queensland mean skin thickness was found to range from 5.9 mm in Shorthorns to 8.3 mm in Africander cattle. In New South Wales, skin thickness measurements ranged from 5.1 to 6.2 mm in AIS, Friesian, Jersey, Guernsey, and Ayrshire cattle (NAY and HAYMAN, 1963).

PAN (1963) and TURNER and SCHLEGER (1970) estimated the skin thickness from the weights of biopsy samples. In New South Wales in Jersey cows the mean thickness was 212 mg and in Sahiwal cows 337 mg (PAN, 1963). In Queensland mean weights were found to range from 332 to 363 mg in Herefords and Shorthorns and from 407 to 449 mg in Africander × Hereford and Shorthorn crosses.

2.2.3. *Repeatability and heritability of some hair follicle and sweat gland characteristics*

Repeatability estimates of hair follicle and sweat gland density measurements have been found to be between 78 and 95% (DOWLING, 1955; NAY and DOWLING, 1957). NAY and DOWLING estimated the repeatability of sweat gland volume at·81%.

JENKINSON et al. (1975) estimated the repeatability and heritability of hair follicle length, depth and slope of the hair, and for sweat gland length, diameter, shape, and volume in Ayrshires and Friesians in Great Britain. The average repeatability was rather high (50–70%) for all characters except angle of slope of the hair (18%). The angle of slope of the hair is obviously a character of low reliability. Heritability estimates for sweat gland characteristics varied from 0.45 to 0.60. Hair follicle characteristics showed less genetic variation (0.15–0.40).

BARKER and NAY (1964) estimated in Jersey cattle in New South Wales the heritability for sweat gland diameter at 60 per cent and for sweat gland volume at 47 per cent. TURNER et al. (1962) estimated in beef cattle in Queensland the heritability of total follicle number/animal to be 29 per cent.

2.2.4. *Interrelationships of some hair follicle and sweat gland characteristics*

JENKINSON and NAY (1968) calculated correlation coefficients between hair follicle and sweat gland characteristics. Their results indicated that animals with deeper hair follicles tend to have longer hair follicles and longer sweat glands, and that longer sweat glands tend to have wider diameters. In 1972 JENKINSON and NAY concluded that there was a tendency for animals with a large L/D ratio also to have a high FD (follicle depth) value.

PAN et al. (1969) found negative correlations (-0,7–-0,8) between sweat gland population density and sweat gland volume.

2.2.5. *Effect of age and body weight*

JENKINSON et al. (1975) mentioned that animals under 2 years of age had shorter and shallower hair follicles and smaller sweat glands than older animals. Earlier work (JENKINSON and NAY, 1968) had shown that in cattle over 2 years of age skin measurements did not vary appreciable with age. JENKINSON and NAY (1968) conclude therefore, that cattle skin has an adult structure by the time the animal is about 2 years old. Skin thickness and the relative thickness of the papillary layer is also independent of age in adult animals (DOWLING, 1955; WALKER, 1960).

In cattle, the total number of follicles is determined before birth (LYNE and HEIDEMAN, 1959). Therefore the number of hair follicles per unit area of skin decreases as the animal grows older because the skin stretches. This follows also from the data of FINDLAY and YANG (1950) and DOWLING (1955) (Appendix 2).

TURNER et al. (1962) found that the follicle density (on the midside) decreases as the animal's body weight increases according to a power of body weight very close to two-thirds. They recommend reporting the follicle densities that apply to a standard live weight of 1000 lb.

These findings suggest that in reporting follicle densities the body weights of the sampled animals should at least be given. The figures for follicle density reported in Appendix 2 are of little comparative value, even from animals in the same environment, sampled at the same age, because it is likely that there are differences in body weight between the test groups.

2.2.6. *Sex differences*

The results obtained by JENKINSON and NAY (1968) (Appendix 1) show that steers have smaller sweat glands than cows, which in turn have smaller glands than bulls. The shape of the sweat gland and the hair follicle depth is the same in bulls, steers, and cows. The hair follicles are longer and thicker in the male than in the castrate; the hair follicle of the cow is thinner than that of the bull.

TURNER et al. (1962) found that the follicle density, corrected for body weight, is higher in male than in female calves.

2.2.7. *Variation in some hair follicle and sweat gland characteristics over various body regions*

FINDLAY and YANG (1950) measured the number of follicles per sq. cm of skin in 21 body regions in Ayrshire cows, and HAFEZ et al. (1955) measured the number of follicles per sq. cm of skin in 16 body regions in 'Egyptian' cattle bulls. The results of these investigations indicated that the follicle density decreases posteriorly.

This is confirmed by the results obtained by PAN (1963): he used 4 four-year-old Jersey cows to study variations in follicle density, sweat gland length, diameter and volume, and in skin thickness and skin shrinkage over the body. They sampled 25 body regions in the Sahiwals and 21 body regions in the Jersey cows. In almost all animals these characteristics varied significantly according to body position. PAN established that the value for the so-called midside position for any of the above-mentioned characters was within 10% of the mean value for all positions. In both breeds the volume of the sweat glands increased posteriorly and the sweat gland and follicle density decreased posteriorly. Skin increased in thickness posteriorly.

PAN et al. (1969) measured follicle and gland density, and sweat gland volume in 5 body regions. The results agreed well with those reported by PAN (1963).

AMAKIRI and HILL (1975) found significant differences in follicle density and follicle depth between various body sites in 4 breeds in Nigeria. The neck, upper limb, and the ventral body sites had high follicle densities; the eye margin, dorsal and midside sites had intermediate follicle densities; low densities were recorded on the horn margin, perineum, and lower limb sites.

2.2.8. *Seasonal variation in some hair follicle and sweat gland characteristics*

NAY and HAYMAN (1963) in New South Wales and JENKINSON et al. (1975) in Great Britain have found that hair follicles are longer and deeper in winter than in summer, and the sweat gland shape does not alter with season. HAYMAN and NAY (1958) and NAY and HAYMAN (1963) in New South Wales, and BENJAMIN (1971) in Canada found that the volume of sweat glands was minimal in summer and maximal in autumn and winter. However JENKINSON et al. (1975) in Great Britain could not find seasonal differences in sweat gland volume.

DOWLING (1964) established that skin was thicker in winter than in summer (in New South Wales).

2.2.9. *Effect of pregnancy and lactation*

There is no literature on the effect of pregnancy and lactation on hair follicle and sweat gland characteristics.

2.2.10. *Effect of nutrition*

Little is known about the effect of nutrition on hair follicle and sweat gland characteristics in cattle.

CARTER and DOWLING (1954) and DOWLING (1955) (Appendix 2) found a denser follicle population in animals that had been on a poor diet or were subjected to drought conditions. It is possible that this results from a decrease in body weight.

2.2.11. *Breed differences*

JENKINSON and NAY (1968), after a study of a number of skin measurements (hair follicle length, diameter and depth, and sweat gland length, diameter, shape and volume), concluded that sweat gland shape and hair follicle depth were reliable indices of skin type in adult cattle in a good state of nutrition. They used these measurements as the principal basis to compare the skin structures of European, Asian, African, and American cattle (JENKINSON and NAY, 1972 and 1973). They distinguished two extreme skin types in European cattle:

- type I, with a $L/D < 8.0$ and $FD < 1.5$ mm
- type II, with a $L/D > 12.0$ and $FD > 2.0$ mm.

Type I is characterized by a sac-like sweat gland and shallow-seated hair follicles; this type was found in almost all the cattle of the Jersey breed, and in most African and Asian cattle. Type II is characterized by a serpentine sweat gland and deeper-seated hair follicles; this type was found in the Scottish Highland breed. Type II was not detected in African, Asian and South American cattle breeds. A third skin type (type III: $L/D > 12.0$; $FD < 1.5$ mm) which was not found in European cattle breeds, occurred in a high percentage of South American cattle breeds and in some Asian and African animals. Most of the Friesian animals studied had a skin type intermediate between the two extremes (L/D: 8.27 ± 2.19; FD: 1.67 ± 0.29 mm). AMAKIRI and HILL (1975) in Nigeria found that the hair follicle depth (FD) was greater in Friesians than in the White Fulani, N'Dama, and the Muturu breeds. This confirms the results obtained by JENKINSON and NAY (1972 and 1973). There were no obvious differences of skin types which could specifically be attributed to differences between dairy and beef breeds.

According to BARKER and NAY (1964) the bagginess of the sweat glands of Yersey cattle is further evidence that this breed may have had Zebu-type ancestors.

It has long been thought that sweat gland volumes of *Bos taurus* cattle are smaller than those of *Bos indicus* cattle. NAY and HAYMAN (1956), HAYMAN and NAY (1958), PAN (1963), and ALLEN et al. (1963) found that Sindhi and Sahiwal cattle in New South Wales had larger sweat gland volumes than cattle from some European breeds. However, JENKINSON and NAY (1972 and 1973) found that Asian and African cattle breeds had smaller sweat gland volumes than European cattle breeds (Appendix 1). According to JENKINSON and NAY (1973) this discrepancy may be because the Sindhi and Sahiwal animals in Australia were kept under excellent nutritional conditions in a relatively cooler climate; besides they are of the opinion that the skin characteristics of Sindhi and Sahiwal cattle are not typical of Zebu cattle in general. Sindhi and Sahiwal animals had slightly more convoluted sweat glands and a greater hair follicle depth than other Asian cattle breeds.

NAY and HAYMAN (1963) found significant differences between 5 breeds in Australia in sweat gland shape and sweat gland volume (Appendix 1).

In various European breeds the follicle densities in mature animals in good condition range from 650 to 1520 per cm^2 (Appendix 2). In contrast, the mean number of follicles in mature *Bos indicus* cattle and in mature *Bos indicus* × *Bos taurus* crosses ranges from 1110 to 1650 per cm^2 (Appendix 2). But the material presented in Appendix 2 is insufficient to establish that there are real breed differences in follicle density, because the data came from animals with different body weights. However, TURNER et al. (1962) have established that Africander crossbreds did not differ from Herefords and Shorthorns, but Brahman crossbreds were 20% higher in follicle density, when adjusted to 1000 lb body weight (Appendix 2).

According to the investigations of PAN (1963), TURNER and SCHLEGER (1970) and DOWLING (1964), the skin of *Bos indicus* cattle is thicker than that of *Bos taurus* cattle. Contrary to these findings, other workers (WALKER, 1960; LYNE and HEIDEMAN, 1960) could not find significant differences between *Bos indicus* cattle and *Bos taurus* cattle. According to WALKER (1960) the difference between *Bos indicus* and *Bos taurus* is not in the thickness but in the skin histology; the follicles of *Bos taurus* are deeper.

2.2.12. *Summary*

Many reports have been published on hair follicle and sweat gland characteristics in cattle. Results for measurements of the length, diameter, depth and density of hair follicles, and the length, diameter, shape, volume and density of sweat glands are summarized in Appendices 1 and 2.

The hair follicle structure of all the cattle breeds investigated has been found to be basically similar.

The sweat glands have been found to vary in shape from simple sac-like structures to coiled tubes.

JENKINSON and NAY (1968) have established that sweat gland shape and hair follicle depth are reliable indices of skin type in cattle.

In *Bos taurus* cattle there is evidence of considerable genetic variation in skin characteristics, particularly in sweat gland characteristics.

The total number of follicles is determined before birth, therefore their final density is related to body size. The figures for follicle density summarized in Appendix 2 are of little comparative value because it is probable that there are differences in body weight. Besides, in some investigations, shrinkage of the skin sample was not taken into account.

Hair follicle and sweat gland characteristics vary significantly according to body region.

There is little information concerning the effects of sex, season, pregnancy, lactation and nutrition on hair follicle and sweat gland characteristics.

Most attention has been given to breed differences in skin characteristics. JENKINSON and NAY (1972 and 1973) compared the skin structures of a large number of Asian, African, American, and European cattle breeds, using sweat gland shape and hair follicle depth as the principal characteristics for comparison. In most breeds there was a wide range of skin types. European breeds had deeper hair follicles and larger sweat gland volumes than did Asian and African breeds. Contrary to these results, experiments conducted in a temperate zone in Australia indicated that Sindhi and Sahiwal cattle had larger sweat gland volumes than cattle from some European breeds.

The evidence available in the literature is insufficient to establish whether there are real breed differences in follicle density.

In general it can be stated that although considerable data have been gathered about hair follicle and sweat gland characteristics in cattle, much more research is still necessary to provide an overall view of differences arising from genetic and environmental influences.

2.3. HAIR COAT CHARACTERISTICS IN CATTLE

The characteristics of the hair coats of cattle are studied

- to give a morphological description of the hair for comparisons between different breeds and different habitats
- in relation to heat exchange
- in relation to performance
- in relation to adaptation.

The characteristics studied in hair coat research have either been assessments of coats *in situ* or measurements made on hair samples.

2.3.1. *Sampling*

Hair samples are mostly taken from the approximate midside area (see 2.2.1.) of the animal by clipping from measured skin areas (SCHLEGER and TURNER, 1960; TURNER and SCHLEGER, 1970; PAN, 1964 and 1970; PETERS and SLEN, 1964; KASSAB, 1964; FRENCH, 1946; DOWLING, 1956, 1958, 1959; BOSMAN, 1962; LOUW, 1959; BERMAN and VOLCANI, 1961; DOWLING and NAY, 1960; HAYMAN, 1965; HAYMAN and NAY, 1961; YEATES, 1954 and 1955).

LEE (1953) proposed that hair samples should be taken with pliers, modified to pull hair from a small known area of animal skin. This method has been applied by BERRY and SHANKLIN (1961), and BIANCA et al. (1974). It has the advantage that all the hairs pulled from the skin can be mounted and examined through a microscope.

2.3.2. *The classification of hairs*

Various workers (e.g. WILDMAN, 1954; BONSMA, 1949; SCHLEGER and TURNER, 1960; SCHLEGER, 1962; PETERS and SLEN, 1964) have classified hair fibers in cattle subjectively as coarse 'guard' hairs of the outer-coat or fine 'insulating' hairs of the under-coat. This subdivision is based on the subdivision that is made in species with primary and secondary follicles. In these species (e.g. sheep and goats) the fine hairs of the under-coat grow in secondary follicles and guard hairs in primary follicles. BONSMA (1949) and SCHLEGER and TURNER (1960) made separate measurements of hair coat characteristics on outer 'guard' hairs and on the fine hairs of the under-coat. BONSMA (1949) found that in woolly-coated beef cattle it was impossible to distinguish these two types.

WILDMAN (1954) established that the winter coat contains a high proportion of short hairs underlying a longer outer-coat, but in the summer there is no distinct under-coat.

BOSMAN (1962) and BIANCA et al. (1974) classified hair fibres into three arbitrarily chosen hair types:

- thin and short hairs
- fairly long and woolly hairs
- long and thick hairs.

They made this classification to obtain truly representative samples for quantitative examination.

2.3.3. *Some hair coat characteristics*

2.3.3.1. Coat score

In Australia, TURNER and SCHLEGER (1960) have developed a subjective scoring system for the totality of the coat, involving manual handling, as well as the appearance of the coat. This coat score ranges from 1 (very sleek, hairs extremely short and closely applied to the skin) to 7 (hairs very woolly and long) with fractional subdivisions. This assessment of the coat is primarily based on an examination of the coat on the midside.

The coat score can be assessed at any time without the need to measure hairs in a laboratory. According to SCHLEGER and TURNER (1960) the advantages of coat score over any other characteristic are its simplicity and the fact that it refers to the whole coat, thereby taking account of features of coat structure that are lost in hair samples. But this coat score system is subjective, it cannot be precisely described, and does not permit observations by different workers to be compared.

Mean coat scores, recorded in February-March in Queensland, were found to range from 2.7 to 6.1 in Hereford and Shorthorn breed groups and from 1.2 to 3.1 in Africander × Hereford or Shorthorn crosses and Brahman × Hereford or Shorthorn crosses (TURNER and SCHLEGER, 1960; SCHLEGER and TURNER, 1960).

2.3.3.2. Depth of the coat

SCHLEGER and TURNER (1960), BERRY and SHANKLIN (1961), WEBSTER et al. (1970) and BERMAN and VOLCANI (1961) have measured the depth of the coat, i.e. the distance between the surface of the coat and the skin. The depth of the coat can be varied by the operation of the erector pili muscles. At low temperatures, these muscles contract, thus increasing the depth of the coat. With hairs of varying length, errors will arise in defining the surface of the coat.

SCHLEGER and TURNER (1960), WEBSTER et al. (1970) and BERMAN and VOLCANI (1961) measured the depth of the coat with a triangular gauge as described by LEE (1953). In Holstein-Friesian cows in Israel the depth of the coat ranged from 2.3 mm (in summer) to 4.3 mm (in winter) (BERMAN and VOLCANI, 1961). In beef cattle in Canada in winter the depth of the coat ranged from 10 mm to 20 mm (WEBSTER et al., 1970).

BERRY and SHANKLIN (1961) used a small metal scale to measure the depth of the coat (also called coat thickness); in Guernsey cows they found that the average depth of the coat was 10 mm.

The different methods of measuring coat depth must have contributed to the differences in the results obtained for mean coat depth.

2.3.3.3. Medullation

WILDMAN (1954) gives a simple classification of forms of medullae of animal fibres:

(a) Unbroken medullae, in which the medullary substance is continuous along the fibre.

The unbroken category includes the following varieties:

- lattice type. The latticed medulla occupies nearly the whole width of the fibre so that the cortex forms only a narrow ring around the outside. This type is present in the coarse kemp fibres of sheep. In cattle the latticed medulla type does not occur.
- simple unbroken medulla. This has the appearance of a simple continuous central canal, thin or thick, but is not as thick as the lattice type.

(b) Broken or interrupted medullae, in which the medulla is usually quite narrow and is interrupted at irregular intervals along the fibre or only occurs irregularly as fragments in the centre of the fibre.

DOWLING (1959a); SCHLEGER and TURNER (1960); TURNER and SCHLEGER (1970); BENNET (1964) and KASSAB (1964) estimated the degree of medullation from the percentage of the fibres medullated. PAN (1964); DOWLING (1956, 1958); HAYMAN (1965), and BIANCA et al. (1974) estimated the degree of medullation by calculating the percentage of fibres showing medullation, and by calculating the ratio of the medulla diameter to the fibre diameter in completely medullated fibres, or by estimating only the medulla diameter.

Data found in the literature on medullation characteristics are shown in Appendix 3.

Mean percentages of medullated hairs range from 4% in rough-coated Shorthorns in Queensland to 100% in Brahman × Shorthorn and Brahman × Hereford crosses in Queensland, and in some Friesian and MRY cows in the summer months in the Netherlands.

2.3.3.4. Hair diameter, hair length, hair density, and weight of hairs

Appendix 4 gives data from literature on diameter, length, density, and weight of hairs.

There are striking differences between the mean values for hair diameter measurements obtained by the various authors. For instance, in Holstein-Friesian cows in Israel BERMAN and VOLCANI (1961) found that the mean hair diameter in the thigh area was 103 μ, whereas in Switzerland BIANCA et al. (1974) obtained a mean hair diameter of only 38 μ from the shoulder area of Holstein-Friesian heifers. The difference in sampling positions probably accounts for at least some of the differences between the mean hair diameters.

Mean values for hair length measurements have been found to vary between 6 mm in Brahman × Shorthorn bulls in Queensland to 34 mm in MRY cows in the winter months in the Netherlands. Differences in the method of measuring hair length make precise comparisons of the data in Appendix 4 difficult. Hair length is usually measured in millimetres. It is difficult to get a representative sub-sample because of the differences in hair length within a sample. SCHLEGER and TURNER (1960) measured only the length of the longest hairs of the fine under-coat. BOSMAN (1962) and KASSAB (1964) chose to measure the long ('guard') hairs. BOSMAN (1962) found a correlation coefficient of r = 0.83 between the length of the long hairs and the length of the rest of the hairs. BIANCA et al. (1974) classified the hairs in three arbitrarily chosen types (see 2.3.2.) and then measured the length of 10 hairs of each of the three types.

'Hair density' is the number of hairs per unit area of skin. In mature cattle, density estimates range from 750 hairs/cm^2 in Shorthorns in Queensland to 1800 hairs/cm^2 in Herefords in Canada. In Hereford and Angus × Bison cows in Canada hair density has been estimated to be even 5400 hairs/cm^2 (PETERS and SLEN, 1964).

HAYMAN and NAY (1961) found that the proportion of empty follicles rarely exceeded 5‰, and follicle population figures were accepted as being equivalent to hair population figures. In contrast, CARTER and DOWLING (1956) found that the number of hair follicles was not equal to the number of emergent hairs, because varying proportions of the follicle population were quiescent or containing young regenerating hairs. The proportion of these categories present in their investigation ranges as high as 20 percent of the follicle population.

Mean values for hair weight measurements were found to vary between 3 mg/cm^2 in Danish red cows in Bulgaria in summer to 49 mg/cm^2 in Hereford steers in New South Wales in winter. In Hereford and Angus × Bison cows in Canada mean hair weight was 72 mg/cm^2 (PETERS and SLEN, 1964). The weight of hair per sq. cm is mainly determined by the number of hairs and their length and diameter. It can be a misleading measure because an animal with a short coat of thick hairs may have the same weight of hair per unit area of skin as an animal with a coat of long, thin hairs (YEATES, 1965).

2.3.3.5. Felting test

In South Africa BONSMA (1949) has developed a so-called 'felting' test for cattle hair: a sample of hair is moistened and rubbed between the hands. The hair of smooth-coated cattle will rub away while that of woolly-haired cattle will felt and form a firm mass. According to BONSMA, cattle with a felting type of hair do not adapt well to the Tropics.

DOWLING (1956 and 1958) rated the degree of cohesion on a scale ranging from 0 (complete absence of felting) to 5 (maximum felting). In Hereford steers in New South Wales the felting test was found to vary between 0 in summer to 5 in winter. In Zebu cattle in Queensland the felting score was found to be 0 in summer and in winter, and in AIS cattle the score was 0 in summer and 2 in winter (DOWLING, 1958). SCHLEGER and TURNER (1960) rated the degree of cohesion on a scale ranging from 1 (complete absence of felting) to 5 (maximum felting). In Hereford and Shorthorn breed groups in Queensland the felting score ranged from 3.1 to 4.1, and in Africander and Brahman crosses (with Herefords and Shorthorns) the score ranged from 1.0 to 1.8.

2.3.3.6. Colour

SCHLEGER (1962 and 1967) applied a system of scoring coat colours to cattle. He used five standards covering the range of red coats in the field (pale straw colour to a dark rich red). In Hereford and Shorthorn calves in Queensland he found that the colour score ranged from about 3 in winter to about 4 in summer; in Africander × Hereford and Shorthorn crosses, the colour score ranged from about 3 in winter to about 3.5 in summer. SCHLEGER (1962) established that melanin concentration was the chief determinant of coat colour, though the proportion of medullated hairs and the diameter of the hairs also had some influence. According to SCHLEGER (1962) a sample of hairs with large diameters tends to appear dark because there are fewer refracting and reflecting surfaces than in a sample consisting of fine hairs.

2.3.3.7. Miscellaneous hair coat characteristics

SCHLEGER and TURNER (1960) using manual handling and visual observations, have studied the 'body' of the coat (a subjective evaluation of the number of hairs per unit area), the 'handle' of the coat (texture of the coat, as an assessment of the diameter of hairs and the degree of medullation), and the curliness of the coat.

Later (TURNER and SCHLEGER, 1970) they collected hair samples from approximately the same patch of skin during nine successive intervals throughout a year. They estimated the regrowth of the coat, of new (pointed) hairs which appeared above clipping level since previous clipping, and of old (blunt) hairs which were cut at previous clipping, but grew further during the interval. The number of follicles per unit area of skin changes as the animals grow. Therefore TURNER and SCHLEGER expressed counts of pointed and blunt hairs and derived counts of emerging and growing hairs as numbers per 1000 follicles. Mean number of growing hairs per 1000 follicles at 9 sampling dates throughout a year varied from 320 to 390 in Herefords, Shorthorns, and Africander crosses in Queensland. The number of new hairs per 1000 follicles per year varied from 1950 to 2250 in these animals.

2.3.4. *Repeatability and heritability of some hair coat characteristics*

A basic criterion of coat characteristics is that each should be a reliable index of animal individuality. It has been found that the repeatability of coat score between season or between years is about 60% (TURNER and SCHLEGER, 1960; SCHLEGER and TURNER, 1960; SCHLEGER, 1967). These authors also found that coat score was highly heritable (46–63%). SCHLEGER and TURNER (1960) established that in comparison with weight of hair per unit area, medullation and the felting test, the coat score was superior with respect to repeatability and heritability.

SCHLEGER (1962) has estimated the heritability of colour score at 53%.

BERMAN and VOLCANI (1961) mentioned that there was a large variation in depth of the coat, hair diameter, and weight of hair per unit area between groups of daughters of different sires, but they gave no figures.

2.3.5. *Interrelationships of some hair coat characteristics*

In an analysis of the various objective characters contributing to overall coat score, SCHLEGER and TURNER (1960) found depth of the coat and hair diameter to be the most important, followed by the percentage of medullated hairs and the maximum length of fine hairs. Later work (TURNER and SCHLEGER, 1970) showed that animals with sleeker coats (lower coat scores) had more new hairs per 1000 follicles over a year, fewer growing hairs per 1000 follicles, and hairs of greater diameter.

Significant positive correlations are found between weight of hair per unit area on the one hand and density, fibre length, and fibre diameter on the other (PETERS and SLEN, 1964; KASSAB, 1964). However, correlations between fibre diameter and hair number per unit area have been found to be negative (PETERS and SLEN, 1964; BERRY and SHANKLIN, 1961). While diameter and medullation were closely correlated (SCHLEGER and TURNER, 1960; KASSAB, 1964), their independent effects on hair weight were of opposite sign. Thicker hairs increased hair weight but, at the same diameter, medullated hairs, being hollow-cored, reduced hair weight (TURNER and SCHLEGER, 1970).

2.3.6. *Effect of age and body weight*

SCHLEGER (1962) found that the birth coat of Hereford and Shorthorn calves, and of Africander cross calves (Africander × Hereford and Africander × Shorthorn) was completely medullated. In the Netherlands the birth coat of Friesian and MRY calves was found to consist of 99–100% of medullated hairs in all seasons, whereas in their mothers the percentage of medullated hairs varied with season from 64 to 100% (KASSAB, 1964) (Appendix 3). The hair weight per cm^2 of calves was greater and the diameters of their hairs were smaller than those of their dams (KASSAB, 1964). TURNER and SCHLEGER (1960) observed a steady decline in the coat score from young calves to animals 3 years old.

2.3.7. *Sex differences*

In Queensland, coat scores of heifers were found to be lower than those of steers but greater than those of bulls (TURNER and SCHLEGER, 1960). Steers were darker than heifers among Hereford and Shorthorn calves, but the colour of steers did not significantly differ from heifers in Africander cross calves (SCHLEGER, 1962).

In the Netherlands KASSAB (1964) observed no significant differences in coat characteristics between male and female calves at birth.

2.3.8. *Variation in some hair coat characteristics over various body regions*

PAN (1964) studied the variation in some hair coat characteristics over the body in Sahiwal (25 body regions) and Jersey (21 body regions) cows in New South Wales. In both Sahiwals and Jerseys, mean hair length, and hair diameter increased posteriorly. The diameter of non-medullated hairs, of medullated hairs, and of the medulla itself also varied between positions, as did the percentage of medullated hairs. The percentage of medullated hairs was the only characteristic for which the commonly used midside sample provided estimates that were within 10% of the mean over all positions.

In Bison calves, hair from the thigh area averaged significantly less in mean fibre length and more in mean fibre diameter than hair clipped from the midside and shoulder areas (PETERS and SLEN, 1964). These findings possibly explain the differences in hair diameter found by BERMAN and VOLCANI (1961), and BIANCA et al. (1974) (see 2.3.3.4.).

BIANCA et al. (1974) determined coat characteristics in six body regions (shoulder, withers, belly, chest, hindleg, and back sacral) of four heifers each of the Brown Swiss, Simmental and Holstein breeds in Switzerland. The standard deviations of the various characters were lowest within the shoulder samples. So they recommend the shoulder area as the most suitable area for comparative studies. They did not use hair samples from the midside position in their investigation. They found that the hairs of the withers area were long and thick, and explained these features by suggesting that they help protect against rain and snow (longer hairs give a better flow down of water). The hairs of the belly area were less medullated and thinner than hairs from the other body regions. The authors speculated that these features helped preserve body heat in the belly area.

2.3.9. *Seasonal variation in some hair coat characteristics*

There are many reports on seasonal changes in coat characteristics in cattle. Differences in habitats make precise comparisons difficult. Most studies about seasonal changes in hair coat characteristics have been made in Australia in both tropical (Queensland) and temperate (New South Wales) zones.

In Herefords and Shorthorns in Queensland the lowest coat score was found for a short time in mid summer then the coat score rose rapidly during the late summer months to a peak in mid winter (TURNER and SCHLEGER, 1960). The ranking of animals for coat-score was similar throughout the year; animals with short summer coats had also relatively short winter coats.

In Friesian cows in Israel and in Jersey heifers in New South Wales the depth of the coat was found to be least in the summer months and greatest in winter (BERMAN and VOLCANI, 1961; ALLEN et al., 1964).

Large and significant changes are found in the incidence and degree of medullation of the hair at different seasons of the year (Appendix 3). KASSAB (1964) and HAYMAN (1965) established that the summer coat in Friesian and MRY cows in the Netherlands and in Friesian × Brahman cows in New South Wales consisted entirely of medullated hairs. But in Shorthorn groups in Queensland the average percentages of fibres showing medullation was found to range from 30 to 100% in the summer months (DOWLING, 1959a; DOWLING and NAY, 1960) (Appendix 3). In winter, medullation is much reduced (DOWLING, 1958 and 1959; DOWLING and NAY, 1960; KASSAB, 1964; BIANCA et al., 1974) (Appendix 3).

Medullated hairs are much greater in diameter than non-medullated hairs

(PAN, 1964). So, seasonal changes in hair diameter probably closely follow seasonal changes in the degree of medullation. This agrees with results obtained by DOWLING (1959a), BERMAN and VOLCANI (1961), KASSAB (1964), ZDRAVKOV and DRAGNEV (1970), and BIANCA et al. (1974) (Appendix 4), who showed that the hair diameter was greatest in the summer months and least in the winter months. In view of the results described above it is surprising that DOWLING (1958) found that the hairs of Hereford steers in New South Wales had a greater diameter in winter than in summer. HAYMAN and NAY (1961) in New South Wales observed no significant differences in hair diameter between summer and winter coats in *Bos taurus* (Jersey, Red Poll, AIS), but in *Bos indicus* (Red Sindhi, Sahiwal) hair diameter was much greater in the summer coat.

Appendix 4 shows that in all breeds and all habitats reported in the literature, hair length decreased from winter to summer, increased again towards autumn, and reached a peak in late autumn or early in winter (DOWLING, 1958 and 1959; DOWLING and NAY, 1960; HAYMAN and NAY, 1961; KASSAB, 1964; ZDRAVKOV and DRAGNEV, 1970; BIANCA et al., 1974).

In all investigations about seasonal changes in weight of hair per unit area of skin, the hair weighed least in summer and most in winter (DOWLING, 1958 and 1960; HAYMAN and NAY, 1961; KASSAB, 1964; ALLEN et al., 1964; PAN, 1970; ZDRAVKOV and DRAGNEV, 1970; BIANCA et al., 1974) (Appendix 4).

In *Bos taurus* cattle in Australia the felting of the coat also changed with season. In Hereford steers in New South Wales the summer coat did not felt at all, whereas in winter all coats felted to a maximum amount (DOWLING, 1958). In Zebu cattle in Queensland the felting score was 0 in summer and in winter (DOWLING, 1958).

No significant seasonal differences have been found in the number of hairs per sq. cm.

2.3.10. *Effect of pregnancy and lactation*

TURNER and SCHLEGER (1960) failed to reveal any effect of pregnancy and lactation upon coat score in Hereford and Shorthorn cows. Lactating Hereford and Shorthorn cows had lower colour scores than non-lactating cows (SCHLEGER, 1962).

2.3.11. *Effect of nutrition*

Much work has been done on the influence of nutrition on wool growth in sheep. The rate of wool growth (measured as the weight of clean wool produced by a certain area of skin in a certain time) is closely related to nutrient intake (RYDER, 1958; SCHINKEL, 1960 and 1962); a poor diet reduces the rate of wool growth, by reducing the length and diameter of the fibres.

It has long been known that nutrition affects the coat of cattle. But there are only a few investigations dealing with quantitative work on the effect of nutrition on hair coat characteristics. TURNER and SCHLEGER (1960) established that animals given supplementary feed had much sleeker coats than animals at pasture. HAYMAN (1965) studied hair growth in two pairs of Brahman × Friesian cows, one of which was maintained on a high plane of nutrition for twelve months, then on a low plane. Treatment was reversed for the other pair. He found that the winter coat of the undernourished animals developed more rapidly; that in winter and spring the hairs of the animals on the low plane were longer; and that in spring the animals on the high plane had a greater hair diameter. SCHLEGER and BEAN (1973) mentioned that animals on a low plane of nutrition had a straw-coloured woolly coat. After several months on a high plane of nutrition, the woolly coat was shed, and new richly-pigmented hairs were produced.

2.3.12. *Breed differences*

Hereford and Shorthorn cattle in Queensland have longer, thinner and less medullated coats, and much higher coat scores than Africander and Brahman crosses (DOWLING, 1958 and 1959a; SCHLEGER and TURNER, 1960; TURNER and SCHLEGER, 1970) (Appendices 3 and 4). PAN (1964 and 1970) established that Jerseys in New South Wales had heavier hair per unit area of skin, and longer hair than Sahiwals. Sahiwals had a greater medulla diameter than Jerseys.

These findings suggest that *Bos indicus* cattle and their crosses with *Bos taurus* have shorter, thicker, lighter, and more medullated coats than *Bos taurus* cattle.

DOWLING (1959a), and DOWLING and NAY (1960) showed that Shorthorn groups, derived from strains that could be considered to have been bred under conditions leading to adaptation to the conditions of tropical Queensland, had shorter and more medullated coats than the group representing the traditional soft-coated type animal (Appendices 3 and 4).

In Bulgaria, local Iskur cows have been found to have heavier hair coats per unit area of skin, longer hairs, and a greater seasonal variation in hair length, hair diameter and medulla diameter than Danish Red cows (ZDRAVKOV and DRAGNEV, 1970) (Appendix 4). According to these authors these differences indicate that Iskur cows are more adapted to Bulgaria's continental climate than are imported Danish Red cows.

2.3.13. *Summary*

This paragraph discusses some results from descriptive work on hair coat characteristics. Most of the observations were made in Australia both in tropical and temperate zones.

The characteristics studied have either been assessments of coats *in situ* or measurements of hair samples. Assessments of coats *in situ* have included coat score, colour score and coat depth. Studies on Hereford and Shorthorn cattle in tropical Queensland have shown that coat score, a subjective assessment of the whole coat, is a very useful indication of coat type. Hair samples have been measured for characteristics such as medullation (Appendix 3), hair diameter, hair length, hair density, hair weight (Appendix 4) and felting ability. SCHLEGER and TURNER (1960) found that coat score is largely determined by coat depth, hair diameter, percentage of medullated hairs, and hair length.

There is disagreement between authors whether or not the number of hair follicles per unit area equals the number of hairs per unit area.

There is evidence of some genetic variation for a number of characteristics.

Hair coat characteristics vary significantly between body regions.

Although it has long been known that nutrition affects cattle coats, this has never been investigated in detail.

Most attention has been given to seasonal and breed differences. Differences between animals in age, body weight, sex, condition, breed and habitat, and differences in methods of measuring coat characteristics make it difficult to interpret satisfactorily the data on seasonal variation (Appendices 2 and 3). Usually the summer coat has short, thick and medullated hairs, whereas in winter the coat is heavier and the hairs are longer, thinner and less medullated.

Work conducted in Australia has established that *Bos indicus* cattle and their crosses with *Bos taurus* cattle have shorter, thicker, lighter, and more medullated coats than *Bos taurus* cattle.

Overall cattle coats are extremely variable and hair coat characteristics are affected by age, body weight, sex, sampling position, season, nutritional status and breed.

2.4. SHEDDING OF THE COAT IN CATTLE

The hair coat of cattle shows marked seasonal variations; *Bos taurus* cattle normally possess a long, woolly coat in winter, and during summer months their coat is sleek, short and medullated (see 2.3.9.). YEATES (1954 and 1955) concluded, from work with Shorthorns in New South Wales, that the winter coat is an elongation of the summer coat, and shedding of the hair coat in cattle occurs only in spring. His conclusions are based on subjective impressions and do not explain why the coat becomes woollier in autumn and winter. The new summer coat first appears on the head, and neck, gradually extending over the shoulder and back; the lower sides and the belly are the last parts to shed (YEATES, 1955; HAYMAN and NAY, 1961). HAYMAN and NAY (1961) observed two shedding periods, in spring and in autumn, in *Bos taurus* cattle (Jersey, Red Poll, AIS, and Friesian), and in *Bos indicus* cattle (Sindhi and Sahiwal) in New South Wales. Approximately 4 months was required for the complete change from winter to summer coat. In autumn the change in appearance was not as drastic as that which occurred in spring (HAYMAN and NAY, 1961).

The findings of YEATES (1954 and 1955), and HAYMAN and NAY (1961) are based on subjective impressions. Histological data of HAYMAN and NAY (1961) and DOWLING and NAY (1960) from skin samples supported the observations of HAYMAN and NAY (1961). HAYMAN and NAY and DOWLING and NAY (1960) estimated the proportions of active follicles. These counts showed a peak of about 70% of active follicles in autumn and a second lower peak in spring (about 50%). About 20–40% of the follicles were in the growth phase at all seasons of the year. DOWLING and NAY concluded that the winter coat is a new coat, and not an elongation of the summer coat.

Because of the heavy seasonal shedding in spring and autumn, HAYMAN and NAY (1961) assumed that most follicles grow two hairs in a year. This is confirmed by the results obtained by TURNER and SCHLEGER (1970) in beef cattle in Australia. They collected hair samples from the same patch of skin during nine successive intervals throughout a year. The total number of new hairs collected in 12 months was equivalent to 2.2 times the number of follicles. They found a cycle of hair growth 200 days long in hairs initiated in February-April, and 110 days long in hairs initiated in summer. The annual cycle showed most activity in April-May (autumn), with a subsidiary peak of activity in October (spring). Their results agree with the counts of active follicles made by DOWLING and NAY (1960) and HAYMAN and NAY (1961).

NAY and JOHNSON (1967) determined percentages of active follicles in Friesian bulls in England. They found large percentages of active follicles in all seasons. There was an indication of a peak beginning in June and lasting till October. This suggests that the winter and summer coats may grow and shed gradually (NAY and JOHNSON, 1967).

The club hair is held in the follicle until the papilla has started to produce a new hair. So shedding of a hair and initiation of a new hair are virtually coincident (DOWLING and NAY, 1960; HAYMAN and NAY, 1961; RYDER, 1973).

2.4.1. *Effect of photoperiod on the shedding of the coat*

It has long been thought that seasonal coat changes in cattle are regulated by environmental temperature. But in a number of animal species, such as the mink, ferret, and hare, coat shedding has been found to be influenced by changes in photoperiod, regardless of the temperatures to which the animals were exposed (BISONNETTE and WILSON, 1939; HAMMOND, 1951 and 1952). These findings led to photoperiodic studies of coat shedding in cattle.

YEATES (1954 and 1955) compared the shedding of the coat in Poll Shorthorns in two contrasting photoperiodic environments. Control animals were kept in a stall under natural daylength conditions (the observations were carried out at Brisbane, lat. 27° S). The experimental treatment consisted in completely reversing the seasonal trend in length of day. The air temperature remained the same for each group. The coats of the control group remained their normal seasonal pattern, those of the experimental animals went into a reverse phase, being long and woolly in the summer and sleek and short in the winter.

The hair coat of a group of Hereford steers, exposed to diminishing daylight gradient, was found to be longer and woollier than the smooth hair of a control group (BOSMAN, 1962). LOUW (1959) established that a sudden and large change in the photoperiod was more effective than a small gradual change, with regard to hair growth response in cattle.

These findings suggest that when cattle are transferred from temperate to equatorial regions, where daylength is virtually the same throughout the year, European cattle will have problems in adapting to the light conditions. YEATES (1958) conducted an experiment to investigate the effect of the equatorial photoperiod on coat shedding. He maintained Shorthorns for periods of up to 21 months in a light environment artificially adjusted to provide 12 hr 50 min of light daily. The initial coat reaction of several groups of these Shorthorns differed according to the season in which they entered the experiment. After a time, however, (about three months) all the cattle grew, and thereafter permanently maintained, a similar coat, characterized by intermediate length and furry appearence.

From the work of YEATES (1954 en 1955) in New South Wales it followed that most animals (Poll Shorthorns) started to shed their winter coat approximately 10 or 12 weeks after the shortest day. In the study made by HAYMAN and NAY (1961) in New South Wales this period was slightly shorter (5 to 10 weeks). In Israel, changes in coat characteristics started much earlier, not later than 5–6 weeks after the shortest day (BERMAN and VOLCANI, 1961). In goats and wild sheep, it has been found that follicles begin to become inactive in September after the autumn equinox (RYDER, 1966 and 1971). According to RYDER the autumn equinox seems to be important in setting the biological clock that controls the annual hair growth cycle. The spring equinox was a less regular marker.

The finding that the normal seasonal coat changes owe their control to a changing photoperiod, does not exclude the possibility that other environmental factors might also exercise some influence on coat changes.

2.4.2. *Effect of temperature on the shedding of the coat*

There are also a few studies dealing with the effect of temperature on the shedding of the coat.

BLINCOE (1956) at the Missouri climatic laboratory observed a decrease in hair weight per cm^2 with increasing temperature, under constant conditions of daylength. In Maryland Dairy Shorthorn heifers, kept in a psychrometric chamber at 90°F from December to July, shed their winter coat in January and secondary shedding occurred in April. The photoperiod in the chamber simulated natural daylight. A control group, housed under prevailing ambient conditions, shed the winter coat in April (MCDOWELL et al., 1960). MURRAY (1965) compared spring shedding in Aberdeen Angus steers maintained in two environments experiencing a similar photoperiod (lat. 32°S), but different seasonal temperatures. The animals in the warmer climate shed their winter coats earlier than the animals maintained under cooler conditions. BERMAN and VOLCANI (1961) studied Holstein Friesian cows in three different temperature regimes, all at the same latitude, in Israel. Mean hair length and depth of the coat were smallest in the region with the highest air temperatures. These coat characteristics also decreased earlier in the region with the highest air temperatures with approaching summer. In Canada groups of four heifers were kept over winter at 20°C or outdoors with and without shelter (WEBSTER et al., 1970). The winter was exceptionally severe: mean January temperature was -28°C. Growth of new hairs was similar in all groups. Hair weight per unit area and coat depth in the animals kept outside were almost twice that of the animals kept at 20°C. WEBSTER et al. assumed that the animals kept outside had a higher hair density, and they explained the increase in hair weight per unit area as a consequence of reduced shedding. However, they did not measure hair densities. It is possible that the increase in hair weight was caused by the increase in coat depth.

These findings suggest that although day-length appears to be the major influence initiating shedding, temperature can modify the seasonal loss of the winter coat.

2.4.3. *Effect of nutrition on the shedding of the coat*

YEATES (1958) and HAYMAN (1965) have studied the effect of nutrition on the shedding of the coat. YEATES (1958) compared coat changes of an experimental group of four undernourished Shorthorn heifers (average gain of 0.14 lb a day) with those of a control group of four well-fed heifers (average gain of 1.00 lb a day). Three of the four animals in poor conditions retained their winter coats through the summer months, and their hair appeared lifeless and bleached. One animal's hair and shedding were normal, despite low nutrition. After return to full feed, the other three animals also shed normally. HAYMAN (1965) found that the winter coat of undernourished Brahman × Friesian cows developed more rapidly, that the winter coat grew longer, and that it was carried later into the spring than the coats grown by well-fed animals.

These studies demonstrate that spring shedding may be delayed by nutritional stress.

2.4.4. *Summary*

In cattle most hair coat characteristics change with the season. It is remarkable that there are two opinions on the shedding of the coat. According to YEATES (1954 and 1955) the winter coat is an elongation of the summer coat and shedding occurs only in spring. On the other hand HAYMAN and NAY (1961) observed two shedding periods: in spring and in autumn. Both opinions are based on subjective impressions.

Australian workers, using skin samples and by clipping hair samples from the same patch of skin during a number of successive intervals throughout a year, found that all the follicles grow two hairs in a year. They concluded that the winter coat is a completely new coat.

It has long been thought that seasonal coat changes in cattle are regulated by environmental temperature. From work of YEATES (1954 and 1955) with Shorthorns in New South Wales in Australia it followed that daylength is the major influence initiating shedding. YEATES (1958) has also shown that in a light environment simulating the equatorial photoperiod the natural hair growth cycle of Shorthorns is disrupted; all the animals grew a furry coat with hair length intermediate between summer and winter coats.

Many organisms use daylength to orient themselves to change of seasons, because in most cases temperature is not a reliable measure for the course of the seasons (Bünning, 1964; Lofts, 1970).

Studies dealing with the effect of temperature on the shedding of the coat showed that in environments with a similar photoperiod animals maintained under warmer conditions shed their winter coats earlier then animals under cooler conditions.

Studies about the effect of nutrition on the shedding of the coat demonstrated that spring shedding may be delayed by nutritional stress.

It can be concluded that daylength is the major influence initiating shedding, whereas temperature and nutrition can modify the shedding in spring.

2.5. HAIR FOLLICLE, SWEAT GLAND, AND HAIR COAT CHARACTERISTICS IN RELATION TO PHYSIOLOGICAL MECHANISMS

This chapter discusses the relationships between follicle, sweat gland, and hair coat characteristics on the one hand, and thermal exchange, performance, and adaptation on the other, and attempts have been made to link some of these studies with others discussed in 2.1., 2.2., 2.3., and 2.4.

2.5.1. *Hair follicle, sweat gland, and hair coat characteristics in relation to heat exchange*

According to Skuldt et al. (1975) the possible avenues of heat transfer in the coat are conduction through the hairs, convection and conduction through the air in the coat, radiation within the coat and to the environment outside the coat, and evaporation. According to Davis and Birkebak (1975) in the absence of direct solar radiation or convective energy transfer, the most important mechanism of (nonevaporative) energy transfer through an animal's coat is conduction through the air in the coat. Moen (1973) considers that usually in mammals conduction is the most important method of heat transfer at the base of the hairs, because the hairs are tightly packed together and there is little air movement. However, Skuldt et al. (1975) have found that radiation and conduction are of about equal magnitude deep in the coat near the skin. Heat transfer from the surface of the hair coat proceeds principally by radiation and convection.

The heat flow from the animal to the environment is inversely proportional to the insulation of the coat. The insulation of the coat may be written in the form $I = (T_s - T_h)/H_s$ where H_s = sensible heat loss, T_s = skin surface temperature, T_h = hair surface temperature. Over 95% of the volume of the hair coat is occupied by entrapped air and this greatly affects the insulation of the coat (Bianca, 1968).

There are two types of convection. In forced convection air blows over the animal, or the animal's own movement produces a local air current (Blaxter, 1962). In free convection small air streams rise from a warm environment. According to Davis and Birkebak (1975) free convection is not an important mechanism of energy transfer within a coat. Forced convection varies with air velocity. KIBLER and BRODY (1954) have shown that winds of 4 m/s increased the non-evaporative heat loss of cows by about a third. BLAXTER and WAINMAN (1964) found that even a mild wind of 0.7 m/s compared with still air of 0.2 m/s reduced the insulation of winter coat in steers. Convection also varies depending on the direction the wind blows on the animal. BENNET (1964) showed that insulation of the coat in a 4.7 m/s wind parallel to the direction of the hair fibres was similar to that in still air, but wind perpendicular to the coat greatly reduced the insulation.

The thermal insulation of the hair coat can be changed by piloerection. In steers, piloerection increased wintercoat depth by about 30% (BLAXTER and WAINMAN, 1964). GONZALEZ-JIMINEZ and BLAXTER (1962) measured the insulation of calf coats both when flat and when erected in response to cold. The flat coat, which was 12 mm thick, had an insulation of 5.5°C/Mcal m^2 24 hr. When erected, although thickness was almost doubled (23 mm), insulation increased to only 7.7°C/Mcal m^2 24 hr. According to MOEN (1973) in wind the increase in the insulation layer by piloerection is partly offset by the greater openess of the coat. More heat is lost through this more open hair layer because of increased penetration by wind and subsequent convective heat loss.

Radiation striking the coat of an animal may be reflected, absorbed within the coat, or transmitted to the skin (CENA, 1973).

RIEMERSCHMIDT and ELDER (1945) were the first to consider the significance of coat colour with regard to aspects of absorption and reflection of incident solar radiation. They established that white or cream-coloured hair absorbs less solar radiation (rays of medium wavelength and rays of long wavelength) than dark hair, and reflects more. The short-wave rays are effectively resisted by yellow, reddish-brown and black colours (BONSMA, 1949). CENA (1966) reported reflectivity values for live cattle and horses ranging from 0.1 for dark coats to 0.42 for white coats.

HUTCHINSON and BROWN (1969) measured the absorptivity of solar radiation (in the wavelength range 0.3–3.1 μm) using dried samples of white, brown, and black cattle coats. All the samples had a high absorptivity in the ultraviolet range. White coats had a low absorptivity in the visual range, whereas coloured coats had a high absorptivity in this region; in the infra-red range, no coats absorbed much radiation. They found that radiant heat penetrated deeper in a white coat than into coloured coats, that is, penetration is inversely related to absorption. At low air movements the difference in absorption outweighed the difference in penetration. So in still air, heat load was greater in coloured than with white coats (the coats were of similar thermal insulation), but at high air movements the effect of colour on heat load was small.

CLARK and CENA (1972) demonstrated that when a black-and-white cow was in the shade, its surface temperatures were almost uniform. When moved into sunshine the difference between the surface temperatures of the black and white coat areas was as much as 8°C. According to CENA (1966) skin temperatures beneath black and white areas follow a similar pattern with a smaller amplitude.

SCHLEGER (1962) established that within the range of red colours (pale straw to a dark red) of Herefords, Shorthorns and crosses between these and the Africander in tropical Queensland, there was no tendency for darker animals to have higher rectal or skin temperatures.

Cutaneous evaporation requires an initial change of state from liquid to vapour at the skin surface and the subsequent diffusion of the vapour into the ambient air. Cattle have a S-shaped cutaneous evaporation curve in response to rising environmental temperature. As the environmental temperature rises, the proportion of non-evaporative cooling falls. At environmental temperatures around 32°C about 80 per cent of the heat loss is due to evaporative cooling (KIBLER and BRODY, 1950). When air temperature is the same as body temperature, body heat can only be lost by vaporization.

KIBLER and BRODY (1950) showed that cutaneous evaporation in adult Jersey and Holstein cows began to rise sharply at an environmental temperature of about 18°C, reaching a maximum at about 28°C. Zebu cattle reached the vaporization peak at 35°C. FINDLAY and ROBERTSON (1964) investigated evaporation moisture loss in 2 castrated bull calves. In one animal increased moisture loss was apparent at 20°C and in the other animal it did not occur until 25°C.

BIANCA (1959) found that the heat loss of calves exposed to hot, humid conditions (40°C dry-bulb and 38°C wet-bulb) was severely restricted. Increasing the air humidity suppresses cutaneous evaporation by reducing the water vapour pressure gradient, between the skin and the air. However, at moderate humidities the effect of humidity on cutaneous evaporation is much smaller than might be expected. MCLEAN (1963) and MCLEAN and CALVERT (1972) found that variations in relative humidity between 35% and 75% have little effect on the rate of evaporation.

Most of the work on cutaneous evaporation rates has been carried out on animals in climatic-chambers, under well-controlled conditions (with regard to temperature and humidity). In the field, solar radiation is also important, and there are daily and seasonal cycles of thermal conditions. MURRAY (1966) established that under field conditions, cutaneous evaporation rates are almost twice those obtained during climate-laboratory exposures, although the animals had lower rectal temperatures. He maintains that direct sunshine, even in quite mild temperatures may initiate sweating in cattle.

At environmental temperatures up to about 20°C the rate of cutaneous evaporation in calves is uniform over the whole body surface (MCLEAN, 1963). At higher environmental temperatures, however, cutaneous evaporation varies significantly between various body regions. The evaporation rate seems to decrease posteriorly and ventrally; the shoulder region having a particularly high rate (PAN et al., 1969; MCLEAN, 1963; BERMAN, 1957; MCDOWELL et al., 1961; MCDOWELL et al., 1955). The areas with the highest evaporation rates are those that under natural conditions might receive the greatest incidence of solar radiation, and are also those areas with the sleekest coats (see 2.3.8.).

With regard to breed differences work from the Missouri climatic laboratory (KIBLER and YECK, 1959) has indicated that Shorthorn heifers have a higher cutaneous evaporation rate than Santa Gertrudis or Brahman heifers, but it was found that the evaporation rate of the Brahman continued to rise as air temperature increased, whereas the Shorthorns showed no change above 27°C. In Australia, Jersey heifers were found to have greater cutaneous evaporation rates than Zebu heifers at moderate temperatures, but Zebus had greater evaporation rates under hot room conditions (ALLEN et al., 1963). SCHLEGER and TURNER (1965) have established that sweating rates are lower in Brahman crosses than in Hereford × Shorthorn steers under mild conditions, but higher under hot conditions. AMAKIRI and MORDI (1975), working in Nigeria, found higher evaporation rates in White Fulani compared to the Friesian cattle.

These reports show that at high air temperatures Zebu cattle and their crossbreds have higher sweating rates than *Bos taurus* cattle.

Not all investigators have found higher sweating rates in Zebus and Zebu crossbreds in hot environments. KIBLER and BRODY (1952) at the Missouri climatic laboratory found no differences in maximal sweating rates between Jersey, Holstein, Brown Swiss, and Brahman cows. ALLEN (1962) under hot room conditions established that Zebus, Jerseys and their crossbreds show similar maximum sweating rates. Similar results have been obtained by MCDOWELL et al. (1955), who found no significant differences for sweating rates between Jersey and Sindhi × Jersey crossbred cows.

The effect of coat cover on sweating ability has been shown by clipping. BERMAN and KIBLER (1959), and MCLEAN (1963) reported that clipping depresses evaporation. This decrease in cutaneous evaporation is probably the direct result of the fact that non-evaporative heat loss increases. In contrast to the results described above, BERMAN (1957), possibly under hotter conditions, found that clipping increases cutaneous evaporation. And BIANCA (1959) showed that clipped calves tolerate the same hot environment (41°C) better than they did before they were clipped. Above approximately 38°C, when heat loss by conduction, convection and radiation is blocked, coat cover probably strongly affects the efficiency of evaporative cooling.

The physical hair characteristics influence the transfer of energy from the skin to the environment.

It has generally been assumed that in mammals the greater insulation value of the winter coat in comparison with the summer coat is caused by the greater hair length and coat depth of winter coats (HART, 1956; HAMMEL, 1955).

TREGEAR (1965) measured the heat loss from excised pieces of pelts of rabbits, horses, and pigs at various wind speeds. He found that the thermal insulation of fur depends greatly on the hair density (he did not take account of other hair coat characteristics) and on the wind velocity; if there were fewer than 1000 hairs per square cm, a 4.1 m/s wind penetrated deep into the fur, but at greater hair densities a 8.3 m/s wind penetrated only a little way into the fur. According to MOEN (1973) a decreased density of the hair permits a large amount of air movement, so convection increases. According to DAVIS and BIRKEBAK (1975) the wind penetration level is also dependent on the depth of the coat.

According to DAVIS and BIRKEBAK (1974) conduction is directly proportional to the fraction of the volume of the coat occupied by hairs. They predict a decrease in conductivity (the rate of heat flow through an insulating medium per unit depth for each degree of difference in temperature) with decreased hair density due to the lower conductivity of air compared to hair. However, the experiments of SKULDT et al. (1975) who studied radiation and conduction in artificial fur, showed increased conductivity with decreased hair density. They have found that radiation increases as fur density decreases.

For cattle there is little information dealing with the influences of different hair coat characteristics on the transfer of heat. It has been found that external insulation increases with increasing coat depth (GONZALEZ-JIMINEZ, 1962; BLAXTER and WAINMAN, 1964; WEBSTER et al., 1970). They regressed external insulation on coat depth. WEBSTER (1970) found that thermal insulation (C m^2 24 h/Mcal) was related to coat depth (D, mm) and wind velocity (V, m/min) according to the formula $I = 11.78 + 0.24\ D - 0.49\ V^{1/2}$. These authors only used coat depth in their calculations. BERRY and SHANKLIN (1961) measured hair coat characteristics and these characteristics were correlated with measured insulation values; total insulation varied linearly with hair weight and hair length. BENNET (1964) measured the heat flow through dried samples of cattle skin; he found a linear relationship between coat depth and insulation both in still air and in wind parallel to the direction of the hairs. BENNET (1964) also found a highly positive correlation between insulation of the coat and coat score, and highly negative correlations between insulation on the one hand and medullation and hair diameter on the other. Cattle with low coat scores exposed to 32°C and a wind speed of 4.7 m/s dissipated most of their heat production as sensible heat, but animals with thick woolly coats still had to rely mainly on evaporative cooling (BENNET, 1964).

In 1949 BONSMA had already noted that cattle with a felting type of hair always have difficulty in maintaining thermal equilibrium.

DOWLING (1956) made observations on the rate of cooling of animals after exercising in the sun for 30 minutes, to ascertain their ability to dissipate heat. Shorthorn bulls with short, thick, medullated hair tolerated exercise in the sun much better than woolly-coated Shorthorn bulls, when rectal temperatures and respiratory rates were used as indices. The same author (1959a) showed that Shorthorns with long woolly winter coats were not heat-tolerant, whereas the same animals, when clipped, were. AIS animals with medullated coats were relatively heat-tolerant, both clipped and unclipped. DOWLING (1959b) suggested that the medulla may be a critical characteristic of the coat in the regulation of heat dissipation by the animal. The correlation between the incidence of medullation and the rectal temperature was 0.95. According to FERGUSON and DOWLING (1955) and DOWLING (1959b) the thicker medullated hairs enhance air movement at the skin surface, this would allow more moisture to evaporate. Furthermore they are of the opinion that the more medullated the hair, the more effective is the reflection of the infra-red wavelengths.

SCHLEGER and TURNER (1960) do not regard medullation as uniquely significant. Within British breed groups in Queensland they found that coat score showed the largest correlation with skin temperature followed by felting, length, diameter, and medullation (TURNER and SCHLEGER, 1960; SCHLEGER and TURNER, 1960).

Sleek-coated calves tolerated heat better than woolly-coated calves even when all were clipped and thereby equated in respect of coat cover (TURNER, 1962). Turner suggested that this is because of the relationship between coat type and sweat gland size and level of sweat gland activity. Hereford and Shorthorn cattle with sleek coats showed a higher sweating capacity under moderate to high heat stress than rough coated Hereford and Shorthorn cattle (SCHLEGER and TURNER, 1965).

Many reports have been published on the histology of the sweat glands in cattle (2.2.), but by comparison, little work has been done on sweat gland activity in relation to sweat gland morphology.

According to JENKINSON and NAY (1973) there is no relationship between sweat gland shape (L/D) and sweat gland activity. The sweat gland volume decreases after stimulation by heat and adrenalin (FINDLAY and JENKINSON, 1960) and by exercise (HAYMAN and NAY, 1958). Sweat gland volume is also least in summer (HAYMAN and NAY, 1958; NAY and HAYMAN, 1963; BENJAMIN, 1971). The sweat gland volumes of Asian and African cattle breeds are smaller than those of European cattle breeds (2.2.11.) and this may therefore indicate that the former sweat more (JENKINSON and NAY, 1972 and 1973).

The study by PAN et al. (1969) indicated that sweating rate correlates positively with sweat gland population density, but negatively with mean sweat gland volume. But AMAKIRI and MORDI (1975) found a negative correlation between sweating rate and sweat gland density. SCHLEGER and BEAN (1971) concluded that neither mean sweat gland volume nor follicle and sweat gland density directly affect sweating rate. They found that the percentage of hair follicles in anagen and the arterial supply to the sweat gland were most closely related to sweating rate in micro-areas of cattle skin.

2.5.2. *Hair follicle, sweat gland and hair coat characteristics in relation to performance*

Because of the possibility that there may be some relationship (phylogenetical) between the structure of sweat glands and the structure of the mammary gland, various authors have investigated the relationships between skin characteristics and performance in dairy cattle. BURCEV (1937), in a study of 500 Red German cows, found a significant positive correlation between milk yield and the follicle and sweat gland density in the ear. FINDLAY et al. (1950) made a similar investigation on a limited number of Ayrshire cows in Great Britain. They found no correlation.

NAY and JENKINSON (1964) examined various skin characteristics in relation to milk yield in Ayrshire, Friesian, Jersey, and Dairy Shorthorn cows in Great Britain. They found that hair follicle depth was negatively correlated with milk yield, and that the relationships between milk yield and various sweat gland characteristics were not significant. NAY and JOHNSON (1967) investigated the relationship between Relative Breeding Value and some skin characteristics in British Friesian bulls. They found a significant positive correlation between the RBV and the follicle diameter, and a significant negative correlation between the RBV and the follicle depth. NAY and JENKINSON (1964), and NAY and JOHNSON (1967) could not find a physiological explanation for these relationships.

BROCHART and LERICOLLAIS (1974) measured hair follicle activity indirectly in beef cattle in France; they plucked hairs and classified the roots as growing or resting. They found significant positive correlations between the percentages of hair roots in anagen in the summer months and the mean weight gain.

TURNER and SCHLEGER (1960) suggested that the criterion by which the significance of coat characteristics may be judged is their relationship to performance.

BONSMA (1949) was the first to relate coat character to productivity of cattle. He established that smooth-coated Shorthorns lost less weight than woolly-coated Shorthorns under very dry conditions in South Africa.

In Australia (tropical Queensland) TURNER and SCHLEGER (1958) have demonstrated that a low coat score (sleek coat) in calves is associated with a high growth rate, and in breeding cows a low coat score is associated with high fertility and high birth weight of calves. Within British breed groups, coat score was significantly related (r about –0.6) with growth rate (TURNER and SCHLEGER, 1960; SCHLEGER and TURNER, 1960; TURNER, 1962). The genetic correlation between coat score and growth rate was estimated at –0.76 for British breed calves. Within Zebu × Hereford and Shorthorn breed groups there was no significant relation between coat score and growth rate (TURNER and SCHLEGER, 1960). BEILHARZ (1972) reported that Hereford cows with low coat scores were those with a high Maternal Production Index (a measure for the overall productive value of a beef cow). SCHLEGER and TURNER (1960) found significant correlations with growth rate for all coat characteristics they studied. The coat score showed the highest correlation (–0.7), followed by depth (–0.6), diameter (+0.6), and medullation (+0.5). In 1970 TURNER and SCHLEGER reported that only the total number of new hairs produced in a year was significantly associated with gain in body weight. Other components of coat type (such as percentage of medullated hairs, diameter of growing hairs, number of growing hairs, growth rate of new hairs) were not significantly related to gain.

The colour score (intensity of colour) has been found to be positively correlated with body weight gain (SCHLEGER, 1962).

Similar relationships have been established for milk yield. In AIS cows, coat score and colour score were negatively correlated with milk yield, and hair diameter was positively correlated with milk yield (SCHLEGER, 1967). In Italian Friesian cows, milk yield was negatively correlated with hair length and hair diameter (MONTEMURRO et al., 1966). And IKRAMOV (1964) showed that in Friesian cows in Uzbekistan, milk yield was negatively correlated with hair length, hair density, and hair weight per unit area of body surface.

2.5.3. *Follicle, sweat gland and hair coat characteristics in relation to adaptation*

Different authors interpret the term 'adaptation' differently. In short a general interpretation will be given here.

Adaptation can be subdivided into:

A) genetic adaptation
B) physiological adaptation

Genetic adaptation refers to the heritable animal characteristics that favour survival of a population in a specific environment. This may involve evolutionary changes (natural selection) or specific genetic properties (selection by man) (HAFEZ, 1968). LADD PROSSER (1964) defined physiological adaptation as any property of an organism which favours survival in a specific environment, particularly a stressful one.

Physiological adaptation can be divided into

- acclimation, which refers to the functional or structural changes in an animal in response to a single environmental factor, as in climatic chambers (LADD PROSSER, 1964; HAFEZ, 1968; MOEN, 1973)
- acclimatization, which refers to the functional or structural changes in an animal in response to a complex of environmental factors (HAFEZ, 1968; LADD PROSSER, 1964).

The hair coat of cattle is the result of adaptation to the environment.

The fact that *Bos indicus* cattle have shorter, thicker, lighter, and more medullated coats than *Bos taurus* cattle, can be regarded as an example of genetic adaptation. JENKINSON et al. (1975) postulate that the short hair follicles and smaller sweat glands of tropical cattle partly result from natural selection for adaptation to warm environments. JENKINSON and NAY (1973) suggest that when selecting cattle for warmer climates from European breeds, such as the Ayrshire and the Friesian, which have a wide range of skin types, animals with a type I skin (sweat gland shape $L/D < 8.0$, and follicle depth $FD < 1.5$ mm) should be chosen. These animals would have shorter and thicker hairs than those of type II ($L/D > 12.0$, and $FD > 2.0$ mm). This could lead to improved heat tolerance and milk production in the Tropics.

Seasonal changes in hair coat may be regarded as acclimatization. During the summer, animals usually carry a short, thick, and medullated coat, whereas in winter the coat is heavier, longer, thinner, and less medullated (see 2.3.9.). The winter coat has a much higher insulative value. The characteristics of the summer coat allow greater efficiency of evaporative cooling (see 2.5.1.).

As is pointed out in paragraph 2.4. the discovery that the shedding of the hair coat is influenced by changes in photoperiod, suggests that when cattle are transferred from temperate to equatorial regions, where daylength is virtually the same throughout the year, European cattle will have problems in adapting to the light conditions (Yeates, 1958). Bonsma had earlier (1949) stressed the importance of coat type in the successful adaptation of cattle to hot environments. He established that the very-smooth coated Africanders and the smooth-coated Shorthorns and Herefords overcame drought conditions much better than woolly-coated Shorthorns and Herefords. French (1946) mentioned that long matted hair is a characteristic of unthrifty European stock in the Tropics.

Turner (1962) maintains that adaptation to stresses may be reflected in coat type. He bases this conclusion on the fact that coat type is related to the thermal balance of an animal (see 2.5.1.) and on the fact that at the high environmental temperatures to which cattle are subjected in northern Queensland, sleek-coated animals have better growth and reproductive performances than long-coated animals (Turner and Schleger, 1958 and 1960; Schleger and Turner, 1960).

2.5.4. *Physiological interrelationships*

The question of the direction of cause and effect in the relationships between coat type and performance has been discussed by Turner and Schleger (1958 and 1960), Schleger and Turner (1960), Turner (1962 and 1964) and Hayman (1965). They illustrate the possible chains of cause and effect as follows:

a. coat type → efficiency of temperature regulation → thrift

b. thrift → coat type → efficiency of temperature regulation

c.

$$\begin{tikzcd}
& \text{thrift} \arrow[dl] & \\
\text{coat type} \arrow[rr] & & \text{efficiency of temperature regulation} \arrow[ul]
\end{tikzcd}$$

In 2.5.1. the relationships between hair coat and heat exchange are discussed. In Australia Turner and Schleger (1960) have established that coat type is directly related to body weight gain.

Most probably all three chains of cause and effect operate to some extent. The question remains as to which mechanism is the more potent (Turner and Schleger, 1960). Turner (1962 and 1964) and Bianca (1961) speculate that coat type is the outward sign of an inner function related to the physiological status of an animal, notably with regard to endocrine functions and efficiency of energy metabolism.

The hormonal pathways that are known to influence hair growth in laboratory animals and in sheep, and in cattle the seasonal nature of shedding suggest that the endocrine system is involved.

Turner (1964) mentioned that according to commercial cattle breeders in North Australia 'hard' cattle, characterized by short coats, withstand heat, diseases, parasites and hardships of nutritional environment better than cattle with woolly coats, but are slow to fatten and finish under favourable conditions. Cattle with woolly coats, are believed to fatten more readily and produce beef with higher finish, provided conditions for growth are favourable YEATES (1965) stated that in the hotter regions of Australia cattle ranchers have begun selecting within their herds for sleek coated animals.

Intensity of colour is positively correlated with rate of body weight gain (SCHLEGER, 1962). SCHLEGER suggested that melanin concentration, the end-product of a series of enzymic processes, could serve as an index of general enzymic activity; so colour is a reflection of the general metabolic status.

According to SCHLEGER and BEAN (1971) the degree of thyrosinase activity and therefore of melanin production in the follicle is greatest during the period of active hair growth. BERMAN (1960) has shown that thyroxine directly affects rate of hair growth and pigmentation. RYDER (1973) mentioned that the melanocyte-stimulating hormone is inhibited by the hormones of the adrenal cortex. The same hormones also inhibit the initiation of hair growth waves in laboratory animals and hair growth rate in sheep. These findings suggest that hair pigmentation and hair growth are related; both may be modified by the same mechanism.

It has long been known that diet affects the coat of an animal (VAN KOETSVELD, 1954), but there is little precise information regarding the effects of poor nutrition on hair growth. One reason for this is perhaps the difficulty of defining precisely what is meant by the dull, dry, and rugged appearance of the coat of an animal in poor condition. In laboratory animals, adrenal cortex hormones inhibit the spontaneous initiation of hair growth; in sheep adrenal cortex hormones discourage the rate of wool growth; and in cattle TURNER and SCHLEGER (1970) have established that a glucocorticoid will depress the initiation of new hairs. BRADFIELD and BAILEY (1967) have found that in man during protein-calorie malnutrition the number of telogen hair roots increases markedly. Extremely poor nutrition, and diseases are known to cause stresses that stimulate the adrenal cortex. Since an old hair sheds when a new one begins to grow, it is possible that nutrional stress and other stresses can inhibit hair loss and new hair growth. In sheep it is known that correlated changes in follicle and fibre dimensions are brought about by alterations in feeding levels (RYDER, 1958; HENDERSON, 1958). Total matrix cell counts in the wool follicles of a Merino sheep indicated that improved nutrition increased the effective germinal cell population (SHORT et al., 1965). SCHINKEL (1960) studied the mitotic activity in follicle bulbs in one sheep on low and high levels of nutrient intake; he found that the rate of cell production from the follicle bulbs on the high intake was 56% greater than that on the low intake. BERGSTROM and KINNISON (1968) compared wool fibre diameters in parasitized and unparasitized lambs; fibre diameters became smaller in most parasitized lambs.

The local application of l-thyroxine has been found to increase hair growth and hair pigmentation (BERMAN, 1960). BOSMAN (1962) found a positive correlation between hair length and Thyroid Stimulating Hormone. In sheep, thyroid hormones have an important influence on the growth rate of wool, but elongation only is affected, not the diameter of the fibre (ROUGEOT, 1965). Various workers (PREMACHANDRA et al., 1957; BLINCOE and BRODY, 1955; GANGWAR, 1969; JOHNSON and RAGSDALE, 1960; YOUSEF and JOHNSON, 1967) have shown that high ambient temperatures depress thyroid activity in cattle. YOUSEF and JOHNSON (1967) demonstrated that low feed intake, as a result of high temperatures, was not the primary factor that altered thyroid activity: temperature had a direct effect too. ANDERSSON et al. (1964) observed that repeated localized cooling of the anterior hypothalamus in the goat resulted in the growth of a coat similar to that which occurs when the entire animal is exposed to cold for some time. This showed the role played by central temperature receptors in controlling hair length growth.

2.5.5. *Summary*

An animal's coat plays a critical role in the heat exchange between the animal and its environment. The effect of free-convection heat transfer in the coat is negligible. Forced convection varies with air velocity. In the absence of forced convection, conduction through the air in the coat is an important mechanism of energy transfer in the coat. Energy transfer in coats also occurs by radiation and conduction through the coat hairs.

An animal receives radiant heat from objects that are warmer than itself. White coats absorb less radiation from the visible spectrum than dark coats, but radiant heat penetrates deeper in a white coat.

The insultative value of the coat reduces the animal's ability to dissipate heat to its environment. In various animals it has been found that the thermal insulation of the coat depends on the hair length and hair density. In cattle, it has been found that the insulation of the coat is related to hair length, coat depth, coat score and hair weight, and is inversely related to medullation and hair diameter.

In Australia Herefords and Shorthorns with sleek medullated coats have been found to tolerate heat much better (when rectal temperatures and respiratory rates were used as indices) and to have a greater capacity to sweat compared with rough-coated Herefords and Shorthorns. Australian workers have suggested that the medulla may be critical in regulating heat dissipation by the animal.

Various authors have investigated the relations between sweat gland characteristics and cutaneous evaporation. Only sweat gland volume has been found to be (inversely) related to sweating rate. SCHLEGER and BEAN (1971) found that the percentage of hair follicles in anagen and the arterial supply to the sweat glands directly affected sweating rate.

The relations between skin characteristics and performance in dairy cattle have also been examined by various authors. The only consistent relationship found was the inverse relationship between follicle depth and performance. The biological significance of this relationship is not clear.

TURNER and SCHLEGER (1960) have suggested that the criterion by which the significance of coat characteristics may be judged is their relation to performance. Under hot conditions in South Africa and Australia the growth rate and reproductive performance of smooth-coated beef cattle were better than those of woolly-coated beef cattle. In tropical Australia the relations between hair coat characteristics and growth rate in beef cattle have been thoroughly investigated. The coat score showed the highest correlation. Workers in Australia and South Africa have suggested that the coat type reflects adaptation to stresses. Cause and effect in the relationships between coat type and performance can probably best be shown as follows:

$$\begin{tikzcd}
& \text{thrift} \arrow[dl] & \\
\text{coat type} \arrow[rr] & & \text{efficiency of temperature regulation} \arrow[ul]
\end{tikzcd}$$

From this paragraph it is clear that little precise physiological information is available on the relations between coat type, heat exchange, performance and adaptation in cattle.

3. EXPERIMENTS

3.1. METHODS USED TO MEASURE HAIR COAT CHARACTERISTICS

This paragraph describes the methods of measuring hair coat characteristics used in this investigation.

3.1.1. *Sampling*

Hair samples were taken with pliers modified to pull hair from a skin area of 20 mm^2. The hairs were extracted in a fraction of a second by a quick jerk. Our plucking technique was essentially that described by LEE (1953). Usually hair samples are taken by clipping from measured skin areas. But when the hair samples are taken from, e.g. a 10 by 10 cm area (BERMAN and VOLCANI, 1961), a 14 by 14 cm area (KASSAB, 1964), or a 10 by 4 cm area (HAYMAN and NAY, 1961) there is a risk that in the samples short woolly hairs sink down. Therefore precautions must be taken to ensure that the final sample for examination is representative of the original material. The advantages of LEE's method (1953) over sampling by clipping are that all the hairs pulled from the skin can be mounted and that the hair roots can also be examined.

Previous researchers have usually taken hair samples from the midside area. PAN (1963) established that in Jersey and Sahiwal cows in Australia values for follicle density and some sweat gland characteristics for the midside sampling position approximated to the average value for about twenty body regions. Therefore, the 10 subsamples we took on each sampling date came from the same place on the midside (between the last rib and the hipbone) unless otherwise specified. The subsamples were collected in envelopes.

3.1.2. *Measurements of hair coat characteristics*

Hairs range from long to very short (especially samples taken in autumn and winter had a great range of long to short hairs) and differ greatly in diameter and shape. Despite many attempts to do so, hairs cannot be precisely classified into types for example in guard hairs of the outer coat and fine hairs of the under coat on the basis of length and diameter. Therefore we did not distinguish various types of hair macroscopically.

3.1.2.1. Macroscopic measurements

Hair density

We counted the number of hairs in 2 of the 10 subsamples. The average value of these subsamples was used as an estimate of the hair density per 20 mm^2 of skin area.

The standard deviation of the differences between duplicate samplings from 12 animals was found to be 34 hairs per 20 mm^2; the coefficient of variation was 11.3%. Thus the determination of hair density is relatively crude, but the mean figures obtained can show useful trends.

Hair length

When measuring hair length it is difficult to get a representative sampling fraction because of the differences in hair length within a sample. Therefore we measured hair length by the method used by BOSMAN (1962) and KASSAB (1964), based on measurements of only the long hairs in a sample. In each of 5 subsamples the lengths of 10 long hair fibres were measured in millimeters; the mean value of these 50 measurements was taken as the hair length.

Table 1 gives F-ratios for the between subsample variance/within subsample variance for 20 animals. For 16 of the 20 animals the between subsample variance was, at the probability level 0.01, not significantly different from the within subsample variance. Also in 20 animals we estimated the correlation coefficient between the length of the long hairs and the length of the rest of the hairs and found $r = 0.86$.

Table 2 gives the results of hair coat characteristics measured by two persons on samples of 10 animals. Statistical analyses on the paired data for hair length showed there was no significant variation.

3.1.2.2. Microscopic measurements

Medullation and hair diameters were determined from the same five subsamples that were used in the hair length measurements. For microscopic examination the five subsamples were cleaned for 10 minutes with petroleum ether; thereafter they were treated for 18 hours with 10% hydrogen peroxide to bleach the black hairs so that the medulla could be more easily observed. The samples were then washed in water and mounted in glycerol on slides.

Medullation

We classified hairs in three arbitrarily chosen types according to medullation:

- *medullated hairs*, in which the medulla varied from thin to thick and was sometimes, for a small part, interrupted at irregular intervals along the hair fibre;
- *fragmentary medullated hairs*, in which the medulla occurred in short lengths only here and there, irregularly along the length of the hair fibre;
- *non-medullated hairs*.

In the literature the division between medullated hairs and woolly (non-medullated) hairs is usually based solely on the presence or absence of medulla. As was discussed in section 2.5.1. various authors have attached particular significance to the presence of a central medulla canal in a hair because of its effect on heat dissipation. Therefore it did not seem justified to combine fragmentary medullated hairs and medullated hairs in one group.

In each of the five subsamples we took 50 fibres at random and classified them according to whether they were medullated, fragmentary medullated, or non-medullated. The results were expressed as percentages.

In 250 hair fibres classified as fragmentary medullated hairs the medullation only extended about 7% along the fibres; this figure was about 90% in 250 fibres classified as medullated hairs.

Differences in percentage of medullated hairs and percentage of fragmentary medullated hairs as measured by 2 persons on 10 animals were insignificant (Table 2).

Hair diameter

Medullated hairs have bigger diameters than non-medullated hairs. So changes in percentage of medullated hairs and changes in hair diameter are related. Therefore hair diameter data were subdivided into two categories: medullated hairs and non-medullated hairs. We found no differences between the mean diameter of non-medullated hairs and fragmentary medullated hairs. Moreover hair diameter measurements were made at a magnification of × 400, so only a small part of the hair was visible and it was usually impossible to distinguish non-medullated hairs from fragmentary medullated hairs. For these

TABLE 1. F-ratios for the between subsample variance/within subsample variance for hair length, diameter of medullated hairs and diameter of fragmentary medullated plus non-medullated hairs

Animal	Hair length	Diameter of med. hairs	Diameter of frag. med. + non-med. hairs
	F^{4}_{45}	F^{4}_{45}	F^{4}_{45}
1	1.71	0.69	0.63
2	24.44***	1.84	1.08
3	1.98	0.95	0.67
4	3.96*	0.60	0.71
5	1.63	0.99	0.24
6	6.52***	1.05	1.98
7	0.80	1.67	1.26
8	4.95***	0.50	2.58
9	3.59*	0.86	2.03
10	2.39	1.20	0.96
11	3.28*	1.08	1.91
12	2.27	0.57	0.62
13	15.53***	0.99	0.19
14	2.80	0.93	1.10
15	2.76	1.62	2.84
16	2.24	1.16	0.81
17	1.11	1.75	0.28
18	1.29	0.15	2.13
19	3.42*	0.05	1.74
20	2.24	1.16	0.81

*: $p < 0.05$
**: $p < 0.01$
***: $p < 0.005$

TABLE 2. Results of hair coat characteristics measured by 2 persons on hair samples of 10 animals

Hair coat characteristics	Number of pairs	Means		S.D. of the differences	t_9-values
		A	B		
Percentage of med. hairs	10	61.9	63.9	3.0	2.0
Percentage of frag. med. hairs	10	23.6	21.2	3.2	2.2
Diameter of med. hairs μ	10	47.0	47.6	1.7	1.2
Diameter of frag. med + non-med. hairs μ	10	23.6	24.2	1.1	1.7
Hair length mm	10	29.7	29.9	1.6	1.0

Absence of differences was chosen as null hypothesis.
S.D.: standard deviation

reasons we combined the fragmentary medullated hairs and the non-medullated hairs in one group.

The diameter of medullated hairs was determined, by randomly selecting 10 different medullated hairs from each of the 5 subsamples, with an eyepiece with a movable micrometer plus fixed measuring score and centering cross-hair. The mean of these 50 values was taken as an estimate of the diameter of medullated hairs. The diameter of 10 non-medullated or fragmentary medullated hairs in each subsample was also measured using the movable micrometer, and the mean value calculated. The unit of measurement used was the micron.

Diameters were not measured at the tip of the hairs.

F-tests on the data for 20 animals indicated that for both the diameter of medullated hairs and the diameter of fragmentary medullated plus non-medullated hairs, the within subsample variances did not differ significantly from the between subsample variances (Table 1). This proved that our method was satisfactory.

Differences between 2 persons in hair diameter measurements were insignificant (Table 2).

Percentage of anagen hair roots

Hair plucking followed by examination of the extricated root has been used as a simple diagnostic dermatological procedure for many years (MAGUIRE and KLIGMAN, 1964; VAN SCOTT et al., 1957; BRADFIELD et al., 1967; CROUNSE and VAN SCOTT, 1960; ARCHER and LUELL, 1960; ORENTREICH, 1967). Growing fibres can be distinguished from those that have formed brush-ends (resting hairs) by microscopic examination of the proximal ends of plucked samples.

We determined the anagen/telogen ratio by a method used by BROCHART and LERICOLLAIS (1974). Almost immediately after the hairs had been collected, the proximal ends of the hair fibres of two subsamples were cut off and treated with petroleum ether for 10 minutes. The roots were then stained for 30 minutes in a solution of carmine alum (carmine 1 p 100; potassium alum 8 p 100), washed in water and mounted in glycerol. The root sheaths of actively growing hairs stained red, whereas the keratinized brush-ends of telogen roots, which have no living matrix, stayed unstained or were only slightly stained. These criteria permitted the two types of hair roots to be counted. In each of the 2 subsamples 75 fibres were chosen and the proportions of growing hairs to resting hairs were determined.

3.1.2.3. Melanin content

The method we used to measure the melanin content of cattle hair was slightly different from Schleger's method (1962). His method was in turn a modification of the Lea's method (1954). The composition of melanin is still unknown; it has never beenobtained in crystalline form and it is very inso-luble. Lea (1954) found that it was possible to dissolve melanin in melted urea.

Our method consisted of treating a sample of hair with petroleum ether several times. 50 mg of the hair were put into a tube with 3 g urea. This mixture was placed in an oil bath which kept the urea at a temperature just above its melting point (132°C). The mixture of hair and urea was occasionally stirred with a glass rod, and the process continued for 4 hours. At the end of this time 10 ml boiling distilled water was added to the hair urea mixture. To precipitate impurities, the mixture was centrifuged for 10 minutes at 5000 r.p.m. The optical density of the solution was measured on a Beckman-β-spectrophotometer. Melanin has a general absorption spectrum (Fitzpatrick et al., 1958). In Figure 8 the absorbance through a solution is graphed as a function of different wavelengths in the visible spectrum. Schleger measured the extinction at 540 mμ. He did not explain why he measured at this wavelength. We measured the optical densities at a wavelength of 400 mμ, in the range of maximal absorption within the visible spectrum, against distilled water as a blank. The melanin content was expressed as optical density units per 50 mg of hair.

To assess the reliability of this method of determining melanin content we calculated the standard deviation of 38 duplicate analyses of different hair samples; it was 15.9 optical density units. The coefficient of variation was 6.0%. We had agreed in advance that a coefficient of variation of about 5% would be acceptable.

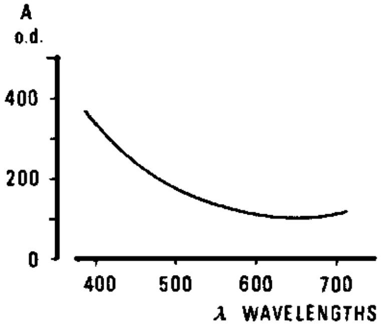


FIG. 8. The absorbance (A) through a solution of hair in urea as a function of different wavelengths.

3.2. HAIR COAT CHARACTERISTICS IN FRIESIAN HEIFERS IN THE NETHERLANDS

3.2.1. *Introduction*

This paragraph presents the results obtained on the hair coat characteristics in Friesian heifers in the Netherlands. These deal with:

- differences in hair coat characteristics between black and white coat areas from the midside
- variation in hair coat characteristics at four different body regions
- seasonal variation in hair coat characteristics
- shedding of the coat
- relationships between body weight gain and some hair coat characteristics.

3.2.2. *Material and Methods*

This section describes the material and methods used in this investigation. A schematic presentation of the material and methods is given in Appendix 5.

3.2.2.1. Animals

The animals sampled in this investigation were 30 Friesian heifers from the experimental farm 'ir A. P. Minderhoudhoeve' of the Agricultural University of Wageningen. These 30 heifers were the progeny of Dutch Friesian cows and 4 Dutch Friesian, and 5 British Friesian sires. The heifers were born between February 4th and April 9th 1974.

Supplementary some observations on shedding of the coat were made on 6 Dutch Friesian heifers from the Department of Animal Production of the Agricultural University of Wageningen. These heifers were born between February 19th and April 20th 1976.

3.2.2.2. Location and Climate

The experimental farm 'ir A. P. Minderhoudhoeve' is located in Swifterbant: a small village which is situated in latitude 52°N, longitude 6°E. According to the climatic classification of GRIFFITHS (1976) the Netherlands are situated in the 'Short-Winter Zone with a uniform rainfall pattern' (mean temperature of 7–11 months $\geq 16°C$; ratio rainfall in driest consecutive 3 months / rainfall in wettest consecutive 3 months > 0.5). Meteorological data for the period of our investigation, January 1975 to March 1976, were obtained from the meteorological observation station 'Flevoland' (Appendix 6), which is located on the farm itself. Mean monthly temperatures ranged from 2.5°C in February 1975 and 1976 to 18.9°C in August 1975. Daylength followed a regular pattern, ranging from 16.40 h in June to 7.50 h in December.

The climate of Wageningen is not much different from that of Swifterbant.

3.2.2.3. Management

From December 1974 until April 1975 the heifers at the 'Minderhoudhoeve' were kept in a loafing barn with cubicles that was open to daylight. During this period hay, silage and concentrates (about 1 kg/head) were provided.

During the grazing period, May 1975 up to November 1975, the heifers received no supplementary feed.

From December 1975, the heifers were again kept in a cubicle barn. About six weeks before calving the heifers were brought into a tying stall, and concentrates equivalent to the requirement for 15 kg milk were provided. In this group of 30 heifers, calving started at the end of February 1976. So at the end of our experiment conditions were not the same for all animals. In the second winter artificial light may sometimes have disturbed the natural daylight pattern.

From December 1976 up to March 1977 the 6 heifers at the Department of Animal Production were kept in a loafing barn with cubicles. During this period they were fed on hay, silage and some concentrates. Weather permitting these heifers were out in the fields during the day.

3.2.2.4. Measurements

Samples from the hair coats of the heifers from the 'Minderhoudhoeve' were taken at regular intervals of 2 months from January 1975 up to March 1976. We took the samples from the black area of the coat at the midside.

In July 1975 we took samples from 14 animals of the black area of the coat as well as samples from the white area of the coat at the midside.

In January 1975, July 1975 and November 1975 in 6 animals we took additional samples from the shoulder, belly and sacrum.

All the samples were analyzed following the procedures described in paragraph 3.1.

The animals were weighed monthly at the same time of the day. The weighing was continued until the heifers reached the 14th week of gestation.

To study hair replacement we bleached the black hairs of the coat on the midside of 6 animals (from the Department of Animal Production in Wageningen) in September 1976. We used a commercial hair lightener; after 30 minutes application the hairs had turned brown. The heifers were first sampled in September 1976 and then at intervals varying from 21 to 60 days. We counted the number of brown (old) hairs and black (new) hairs. In these two categories we measured hair coat characteristics, according to the methods described in paragraph 3.1.

3.2.2.5. Statistical procedures

Differences in hair coat characteristics between black and white coat areas on the midside were tested using t-tests for paired comparisons.

Data on the hair coat characteristics of four body regions were subjected to analysis of variance. Duncan's multiple range test at the 5% level of significance was used to determine individual differences between means.

In the existing literature, the statistical analysis of data on hair coat characteristics is usually analysis of variance. Analysis of variance assumes that all observations are independent. But as our sampling intervals were only a few months apart, this requirement could not be fulfilled. Moreover, analysis of variance and t-tests do not specify what kind of changes occur. Since one of our aims was to investigate seasonal trends, and since our sampling intervals were equidistant we decided to use the method of orthogonal polynomials to analyse seasonal variations in hair coat characteristics. To do this usefully the polynomial must be of fairly low degree.

If a polynomial regression line $Y = a + bx + cx^2 + dx^3 + ex^4 \ldots$ is to be fitted to series of n observations at equal intervals of x we may fit instead the equivalent line $Y = A + Bg_1 + Cg_2 + Dg_3 + Eg_4 \ldots$ where g_r are orthogonal functions of x, with $0 < r < n-1$. Curvilinear regression by fitting orthogonal polynomials is a stepwise procedure with a significance test for each increase in powers of x to ascertain whether the fit has improved significantly.

For each hair coat characteristic two polynomial regression analyses were made: a 'combined' polynomial regression and a 'pooled' polynomial regression analysis. In the combined analysis the between sampling date sum of squares were divided into linear, quadratic, cubic, quartic, and higher-order components. In the pooled analysis polynomials were fitted to the data for each individual animal. The sum of the sum of squares of each animal gave the pooled sum of squares. Now it was possible to make analyses of the heterogeneity between the fitted polynomials. The heterogeneity sum of squares and degrees of freedom were obtained as differences between the pooled and the combined sum of squares and degrees of freedom. This procedure is listed below.

Source of variation		SS	df	MS
Linear regression	pooled	P_l	p_l	
	combined	C_l	c_l	C_l/c_l
	heterogeneity	H_l	h_l	H_l/h_l
Quadratic regression	pooled	P_q	p_q	
	combined	C_q	c_q	C_q/c_q
	heterogeneity	H_q	h_q	H_q/h_q
⋮	⋮	⋮	⋮	⋮

The mean squares were compared with the remainder mean squares by the F-test. When the heterogeneity mean squares proved insignificant the fitted (combined analysis) trend was graphed.

The method of orthogonal polynomials is described by e.g. VAN DER REYDEN (1943), ANDERSON (1971), and DE JONGE (1963).

To describe the seasonal cycle in daylength and in some hair coat characteristics (for the six sampling dates in 1975) we also used the following sinewave:

$\hat{Y}_i = \bar{Y} + A \sin \pi/180\,(30t_i + \beta) + e_i$, (SOLLBERGER, 1970) where
$\hat{Y}_i$ = estimate of Y_i
$\bar{Y}$ = average value of Y
A = amplitude
t_i = time in months
β = phase angle
e_i = error

Pooled correlation coefficients between various hair coat characteristics combining the correlation coefficients within data were calculated by Fisher's z-transformation method.

Estimates of the relationships between body weight gain and various hair coat characteristics, within each of the sampling dates, were determined by multiple regression analysis. The model was: $Y = a + b_1x_1 + b_2x_2 \ldots + b_7x_7 + e_i$ where Y = body weight gain; x_{1-7} = various hair coat characteristics.

Results from the shedding experiment were subjected to non parametric tests against trend (DE JONGE, 1963).

Other statistical procedures used will be mentioned in the text.

Transformations

X^2-tests showed that the distributions of the percentages of medullated hairs, fragmentary medullated hairs and anagen roots, of the hair density and of the melanin content were not normal, and when the data were tested with Hartley's test (DE JONGE, 1963) the results showed that they were not homogenous. Consequently it was necessary to transform these data so we could use classic methods.

We used logarithmic transformation for the hair density and melanin content data, and arcsin transformation for the percentage data. The transformations succeeded in making the distributions of the characteristics normal and the requirement for homogeneity could also be fulfilled. Estimates of means and their standard deviations are given in the untransformed scale.

3.2.3. *Results*

3.2.3.1. Differences in hair coat characteristics between black and white coat areas from the midside

Table 3 gives the results of measurements of the hair coat characteristics of black and white coat areas from the midside. The hair samples were taken in July.

Absence of differences between black and white coat samples was chosen as null hypothesis. The t-values in Table 3 show that within animals, white hair fibres from the midside sampling area were more medullated ($p < 0.005$) than black hairs. The black coat area contained more fragmentary medullated hairs ($p < 0.005$).

The mean diameter of white medullated hairs was less than that of black medullated hairs ($p < 0.005$). The mean diameter of the fragmentary medul-

TABLE 3. Differences in some hair coat characteristics between black and white hairs, within animals
Sampling date: July 1975

Hair coat characteristics	Number of animals (n)	Means		S.D. of the differences	$t_{(n-1)}$-values
		black hairs	white hairs		
Percentage of med. hairs	14	78.4	96.2	12.6	5.3***
Percentage of frag. med. hairs	14	18.2	2.0	11.6	5.2***
Diameter of med. hairs μ	14	43.5	38.4	4.2	5.1***
Diameter of frag. med. + non-med. hairs μ	8[a]	24.3	21.0	3.9	2.4*
Diameter of all hairs μ	14	39.3	37.7	4.0	1.5
Hair length mm	14	24.8	25.6	2.1	1.5
Hair density per 20 mm^2	14	293	286	65	0.4

*: $p < 0.05$
**: $p < 0.01$
***: $p < 0.005$
a: in 6 animals the white coat area contained medullated hairs only
S.D.: standard deviation

lated plus non-medullated white hairs was also less than that of the corresponding sample of black hairs ($p < 0.05$). But because white hairs were more medullated the mean diameter of all hairs did not differ between black and white hairs.

There were no significant differences in hair length and hair density between black and white coat areas.

3.2.3.2. Variation in hair coat characteristics at four different body regions

Figure 9 gives the mean values and their standard deviations of data on the hair coat characteristics from 6 animals for shoulder, belly, midside, and sacrum body regions. The animals were sampled in January, July and November.

Analyses of variance for each sampling date (Table 4) showed significant effects of body region for percentage of medullated hairs, diameter of fragmentary medullated plus non-medullated hairs and hair density in January and November, and in January also for percentage of fragmentary medullated hairs and diameter of medullated hairs. In July there were no significant effects of body region. So in July the coats of the experimental animals were uniform over the body.

On all three sampling dates some differences between animals also were significant.

Individual differences between means of body regions were tested using Duncan's multiple range test (DUNCAN, 1955). The results are presented in Table 5.

TABLE 4. Analysis of variance of some hair coat characteristics for 4 different sampling positions in 6 animals on 3 sampling dates

Source of variation	df	Mean Squares					
		Perc. of med.[a] hairs	Perc. of frag.[a] med. hairs	Diam. of med. hairs	Diam. of frag. med. + non-med. hairs	Hair length	Hair density[b]
January 1975							
Body region	3	572***	254***	86***	34***	37	0.014***
Animal	5	199***	32	5	18***	39*	0.006
Remainder	15	42	16	11	2	13	0.002
July 1975							
Body region	3	48	16	14	–[c]	6	0.001
Animal	5	357***	307***	16	–	27	0.001
Remainder	15	69	49	25	–	10	0.001
November 1975							
Body region	3	247***	61	23	18***	36	0.004
Animal	5	60	30	29	5***	97***	0.002
Remainder	15	51	20	14	0.05	12	0.001

*: $p < 0.05$
**: $p < 0.01$
***: $p < 0.005$
a: arcsin $\sqrt{\%}$ transformation
b: logaritmic transformation
c: half of the samples contained medullated hairs only

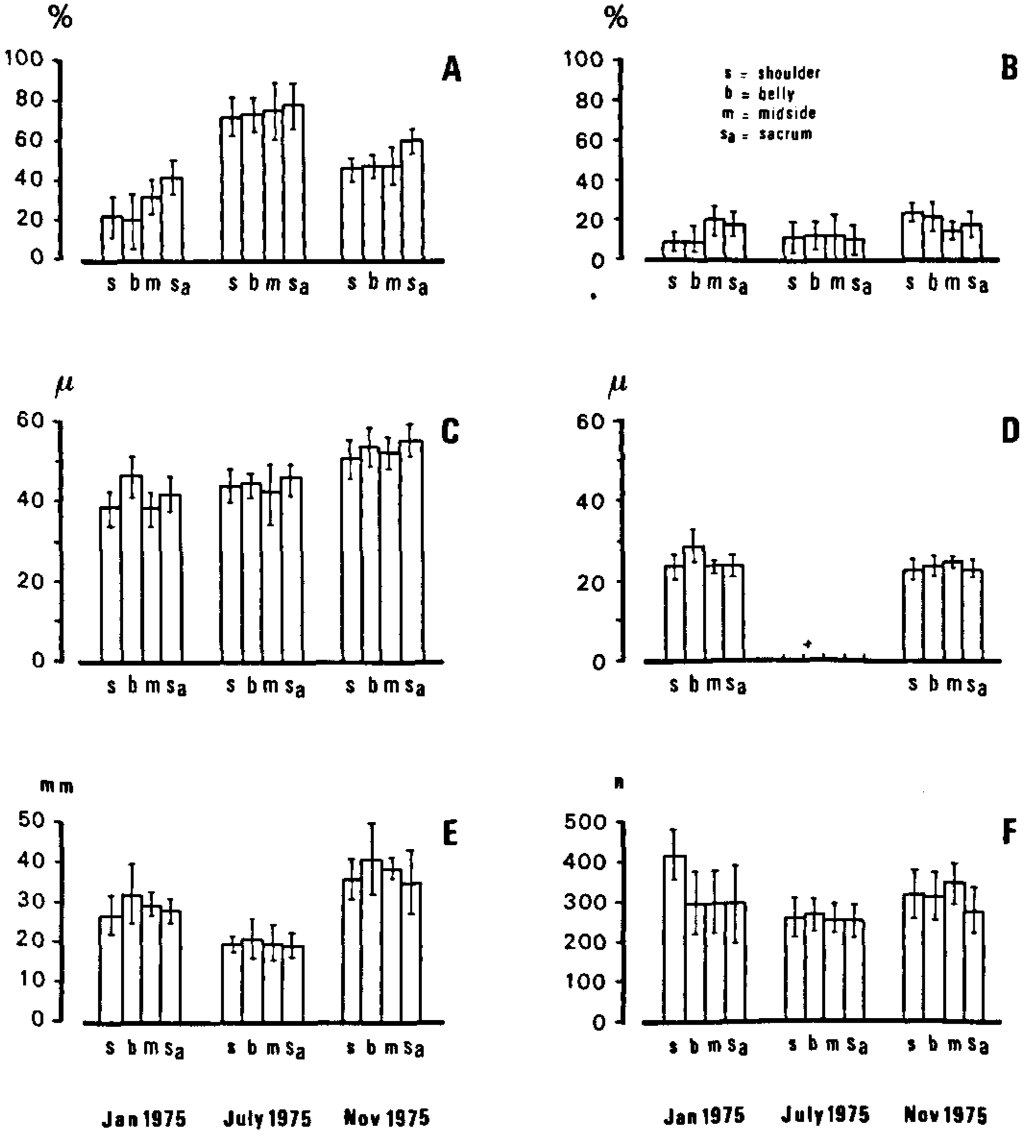


FIG. 9. Mean values and their standard deviations of some hair coat characteristics for 4 different body regions for 6 animals on three sampling dates

A: percentage of medullated hairs
B: percentage of fragmentary medullated hairs
C: diameter of medullated hairs
D: diameter of fragmentary medullated plus non-medullated hairs
E: hair length
F: hair density per 20 mm^2
+: half of the samples contained medullated hairs only.

TABLE 5. Duncan's multiple range test to determine individual differences between means of body regions

Hair coat characteristics	Sampling dates		
	January 1975	July 1975	November 1975
Percentage of med. hairs	sacrum midside shoulder belly	sacrum midside belly shoulder	sacrum midside belly shoulder
Percentage of frag. med. hairs	midside sacrum belly shoulder	midside belly shoulder sacrum	shoulder belly sacrum midside
Diameter of med. hairs	belly sacrum shoulder midside	sacrum belly shoulder midside	sacrum belly midside shoulder
Diameter of frag. med. + non-med. hairs	belly sacrum midside shoulder	a	midside belly shoulder sacrum
Hair length	belly midside sacrum shoulder	belly midside shoulder sacrum	belly midside shoulder sacrum
Hair density	shoulder belly sacrum midside	belly shoulder midside sacrum	midside shoulder belly sacrum

Body regions not underscored by the same line differ significantly from each other
a: half of the samples contained medullated hairs only

In January, the sacrum had the highest percentage of medullated hairs (42%); the low percentages of medulla in the belly and shoulder areas (about 22%) were striking. The belly and shoulder areas also had lower percentages of fragmentary medullated hairs than the sacrum and midside areas. The largest diameters of medullated and fragmentary medullated plus non-medullated hairs were found in hairs from the belly area. The high hair density in the shoulder area was notable: 415 per 20 mm^2, compared with a hair density in the other body regions of about 300 per 20 mm^2.

In November the sacrum had the highest percentage of medullated hairs and the lowest hair density.

3.2.3.3. Seasonal variation in hair coat characteristics

To investigate seasonal trends orthogonal polynomials to the fourth degree were fitted to data on characteristics of hair coat samples taken from the 30 heifers on all 8 sampling dates. Table 6 gives the polynomial regression analyses. Figure 10 gives the graphical representation of the regression lines. The fitted polynomials are an approximation to the real (but unknown) trends. They can only be used for interpolation. The results led to the following being established:

- medullation

Figure 10a shows large seasonal variations in percentage of medullated hairs. The curve shows a peak of about 90% in the summer months with corresponding dips during the winter months of about 47% (1975) and 51% (1976). The percentage of fragmentary medullated hairs in the hair samples was low. Although it was possible to fit a polynomial to the data on percentage of fragmentary medullated hairs, this percentage changed very little during the period investigated (Figure 10b). Figure 10a shows that there is a distinct rhythm in the percentage of medullated hairs. Many seasonal events in animals are timed by changing daylengths. In Figure 11 we fitted mean values of percentage of medullated hairs for the 6 sampling dates in 1975, and daylength data to a sine function. The sine function $\hat{Y}_t = 12.2 + 4.3 \sin \pi/180\ (30t + 260)^\circ$ determined 99.8% of the variance in daylength and the sine function $\hat{Y}_t = 71.3 + 22.3 \sin \pi/180\ (30t + 226)^\circ$ determined 90.9% of the variance in percentage of medullated hairs. These functions indicate that the cycle of percentage of medullated hairs in 1975 was closely related to changes in daylength but with a time lag of 34° (about 1 month).

- hair diameter

The curve of the changes in diameter of medullated hairs indicates a steady increase from July to January (Figure 10c). After January a gradual decrease set in. Polynomials of first, second, and third degree could be fitted to changes in the diameter of fragmentary medullated plus non-medullated hairs; this diameter followed a gradual curve with a dip in June 1975 and a peak in February 1976 (Figure 10d). The diameter of the medullated hairs was about twice that of the non-medullated and fragmentary medullated hairs.

– hair length

The curve for hair length shows large seasonal variations: the hair length decreased gradually from January 1975 until midsummer; towards autumn, hair length more than doubled, reaching a peak in December, and in winter 1976 (during the stall period) hair length decreased rapidly again (Figure 10e).

– melanin content

A second degree equation gave a good fit for the melanin content data. The curve progressively decreases from an initial value of 390 o.d. (optical density units per 50 mg of hair) to 190 o.d. in September 1975, thereafter the curve rises to a value of 310 o.d. in March 1976 (Figure 10f).

– hair density

For hair density the heterogeneity mean squares proved significant, indicating that the curves for each animal were not similar in shape. It could only be concluded that there were significant differences between the sampling date means. Duncan's multiple range test at the 5% level of significance was used to determine individual differences between the observed means:

July 1975	March 1975	Sept. 1975	May 1975	Jan. 1975	March 1976	Jan. 1976	Nov. 1975
270	271	279	280	307	309	323	330

Means (hair density per 20 mm^2) not underscored by the same line differ significantly from each other. So the hair densities in November 1975 and January 1976 differed from the hair densities in March 1975, May 1975, July 1975 and September 1975. In cattle the total follicle number is determined before birth. Therefore the number of hair follicles per unit area of skin decreases as the animal grows older because the skin stretches. Therefore the increase in hair density in autumn is surprising, it indicates that the number of empty follicles is larger in the spring and summer months than in autumn and winter.

– percentage of anagen hair roots

There was a very high percentage of hair roots in anagen phase. The peak was in late autumn (Figure 10h). The expected annual cycle of activity did not occur.

FIG. 10. Polynomial regression curves for 8 different hair coat characteristics from 30 Friesian heifers

A: percentage of medullated hairs
B: percentage of fragmentary medullated hairs
C: diameter of medullated hairs
D: diameter of fragmentary medullated plus non-medullated hairs
E: hair length
F: melanin content
G: hair density per 20 mm^2
H: percentage of anagen hair roots

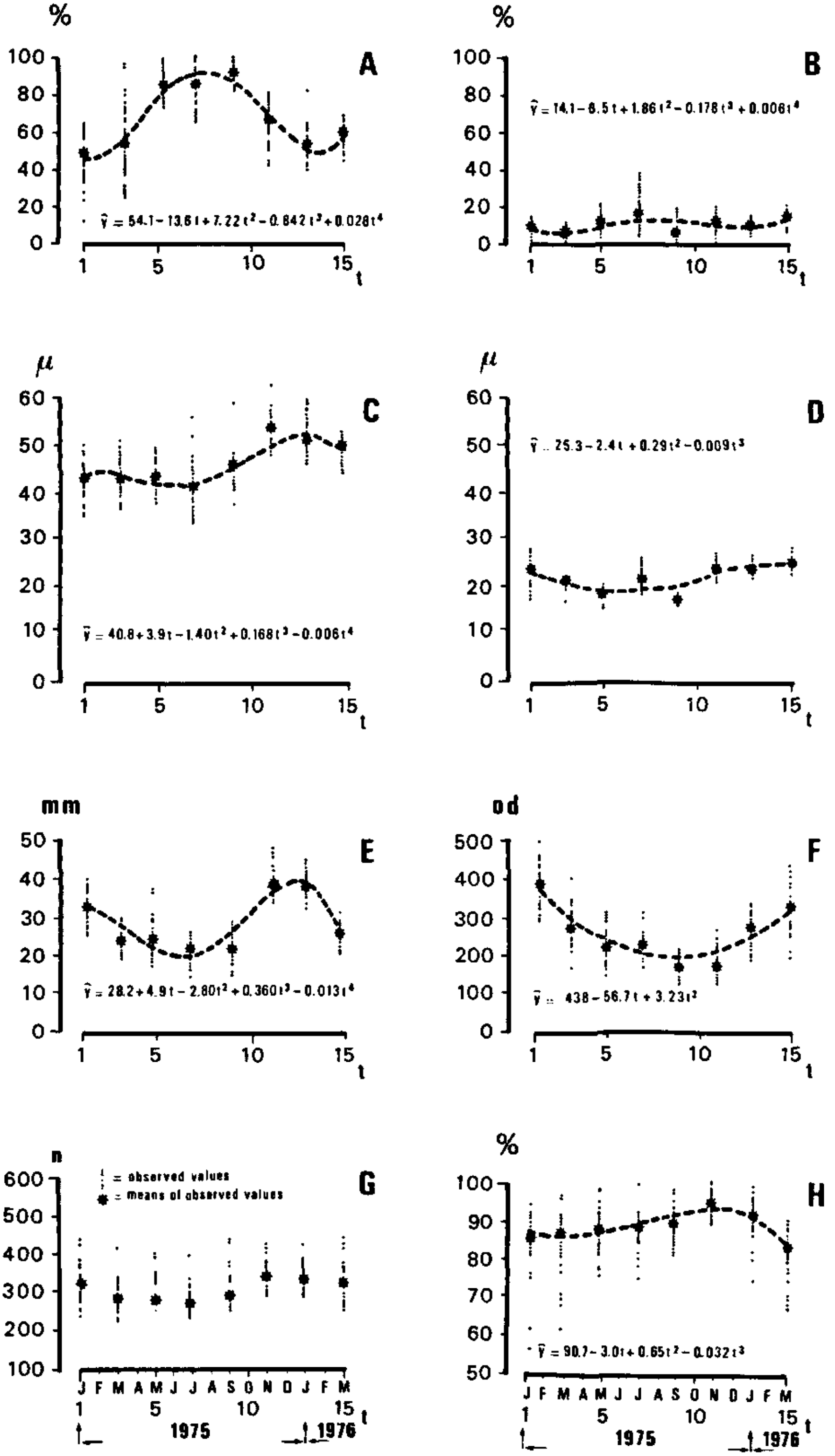

A
%
100
80
60
40
20
0
$\hat{y} = 54.1 - 13.6t + 7.22t^2 - 0.842t^3 + 0.028t^4$
1
5
10
15
t
B
%
$\hat{y} = 14.1 - 6.5t + 1.86t^2 - 0.178t^3 + 0.006t^4$
C
μ
60
50
40
30
10
$\hat{y} = 40.8 + 3.9t - 1.40t^2 + 0.168t^3 - 0.006t^4$
D
μ
$\hat{y} = 25.3 - 2.4t + 0.29t^2 - 0.009t^3$
E
mm
$\hat{y} = 28.2 + 4.9t - 2.80t^2 + 0.360t^3 - 0.013t^4$
F
od
500
400
300
200
100
$\hat{y} = 438 - 56.7t + 3.23t^2$
G
n
600
⋮ = observed values
✱ = means of observed values
J F M A M J J A S O N D J F M
1975
1976
H
%
90
70
50
$\hat{y} = 90.7 - 3.0t + 0.65t^2 - 0.032t^3$

TABLE 6. Polynomial regression analyses for various hair coat characteristics

Source of variation		Perc. of med. hairs			Perc. of frag. med. hairs			Diameter of med. hairs			Diameter of frag. med. plus non-med. hairs		
		SS	df	MS	SS	df	MS	SS	df	MS	SS	df	MS
Linear regression	pooled	1156	29		560	29		1668	29		222	29	
	combined	36	1	36	526	1	526***	1272	1	1272***	159	1	159***
	heterogeneity	1120	28	40	34	28	1	396	28	14	63	28	2
Quadratic regression	pooled	46684	29		999	29		13	29		380	29	
	combined	44108	1	44108***	47	1	47	0	1	0	340	1	340***
	heterogeneity	2576	28	92	952	28	34	13	28	0.5	40	28	1
Cubic regression	pooled	4616	29		281	29		1504	29		148	29	
	combined	4056	1	4056***	46	1	46	811	1	811***	77	1	77***
	heterogeneity	560	28	20	235	28	8	693	28	24	71	28	3
Quartic regression	pooled	13768	29		950	29		680	29		165	29	
	combined	11080	1	11080***	435	1	435***	522	1	522***	12	1	12
	heterogeneity	2688	28	96	515	28	18	158	28	6	153	28	5
Remainder		33948	123	276	1968	123	64	1929	123	16	590	123	5

Table 6 (continued)

Source of variation		Hair length			Melanin content			Hair density			Perc. of anagen hair roots		
		SS	df	MS	SS	df	MS	SS	df	MS	SS	df	MS
Linear regression	pooled	456	29		142267	24		127851	29		508	29	
	combined	350	1	350***	107675	1	107675***	30355	1	30355***	248	1	248
	heterogeneity	106	28	4	34592	23	1504	97496	28	3482***	260	28	9
Quadratic regression	pooled	298	29		780285	24		104572	29		1471	29	
	combined	203	1	203***	730697	1	730697***	17940	1	17940***	1225	1	1225***
	heterogeneity	95	28	3	49588	23	2156	86632	28	3094***	246	28	9
Cubic regression	pooled	6644	29		3543	24		104836	29		1288	29	
	combined	6372	1	6372***	2071	1	2071	37636	1	37636***	1187	1	1187***
	heterogeneity	272	28	10	1472	23	64	67200	28	2400*	101	28	4
Quartic regression	pooled	3801	29		10015	24		14627	29		356	29	
	combined	2680	1	2680***	1528	1	1528	5283	1	5283	311	1	311
	heterogeneity	1121	28	40	8487	23	369	9344	28	334	45	28	2
Remainder		4059	123	33	442208	104	4252	156948	123	1276	11021	123	90

*: $p < 0.05$
**: $p < 0.01$
***: $p < 0.005$

SS: sum of squares
MS: mean squares
df: degrees of freedom

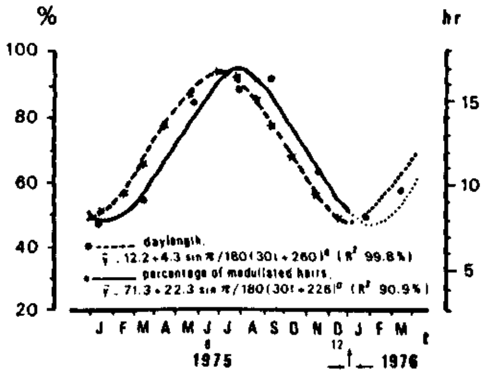


FIG. 11. Relationship between annual variations of daylength and percentage of medullated hairs

Correlation coefficients between various hair coat characteristics

We calculated the correlation coefficients between various hair coat characteristics per sampling date. For each combination of hair coat characteristics we tested the null hypothesis that the 8 r's did not differ significantly from each other. When the null hypothesis was not rejected the correlation coefficients were pooled using Fisher's z-transformation method (DE JONGE, 1963). Only 4 of the pooled correlation coefficients were significant (Table 7). Animals with medullated hairs of greater diameter also had non-medullated and fragmentary medullated hairs of greater diameter ($p < 0.001$), had a lower percentage of fragmentary medullated hairs ($p < 0.05$), and their hairs were longer ($p < 0.01$). The percentage of medullated hairs was negatively correlated ($p < 0.001$) with the diameter of fragmentary medullated plus non-medullated hairs. In general the correlation coefficients were low. This is not surprising, because most hair coat characteristics have different physiological backgrounds.

3.2.3.4. Shedding of the coat

We used the data on the percentage of hair roots in anagen phase and the data on the hair density to calculate the number of growing hairs per unit area of skin (Figure 12). A fourth degree equation gave a good fit for the changes in the number of growing hairs; a dip in the curve occurred in March, there was a large peak in November. In Figure 13 the results of the measurements of hair density and percentages of medullated, and fragmentary medullated hairs

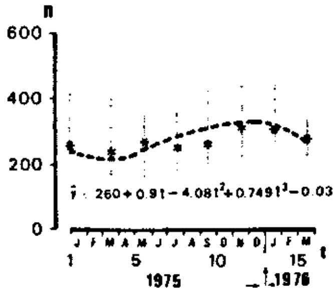


FIG. 12. Polynomial regression curve for the number of growing hairs per 20 mm²

TABLE 7. Pooled correlation coefficients between various hair coat characteristics

	Perc. of med.^{a} hairs	Perc. of frag.^{a} med. hairs	Diameter of med. hairs	Diameter of frag. med. + non. med. hairs	Hair length	Hair^b density	Perc. of^b anagen hair roots
Perc. of frag. med. hairs (216)	–						
Diameter of med. hairs (216)	0.06	–0.14*					
Diameter of frag. med. + non-med. hairs (216)	–0.35***	–	0.37***				
Hair length (216)	–0.03	–	0.23**	0.06			
Hair density (216)	–0.13	–	0.05	0.02	–		
Perc. of anagen hair roots (216)	0.04	0.02	0.02	0.07	0.08	0.03	
Melanin content (204)	–0.13	0.11	0.04	–0.04	–0.03	–0.02	–

The figures within brackets correspond to the degrees of freedom

*: $P < 0.05$

**: $P < 0.01$

***: $P < 0.005$

a: arcsin $\sqrt{\%}$ transformation

b: logarithmic transformation

–: the correlation coefficients differed significantly from each other

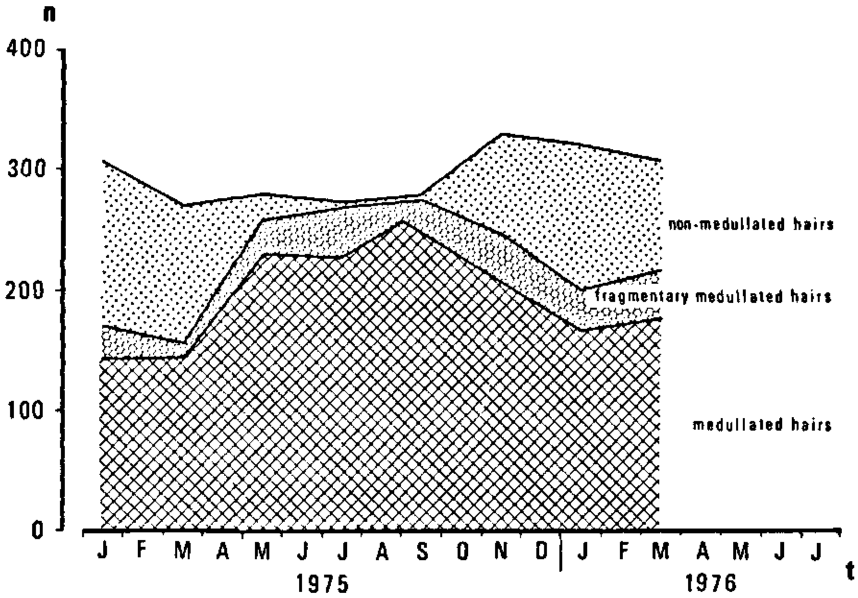


FIG. 13. Hair coat composition per 20 mm² from 30 Friesian heifers, during the period January 1975–March 1976

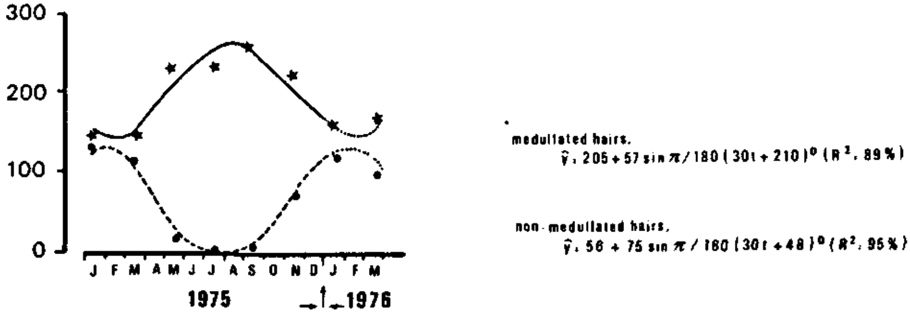


FIG. 14. Seasonal variation in the number of medullated hairs per 20 mm² and in the number of non-medullated hairs per 20 mm²

are combined. This figure shows that both in spring and in autumn large changes occurred in coat composition. The assemblage of sine curves described the seasonal changes in the number of medullated hairs per unit area and in the number of non-medullated hairs per unit area very well. The phase difference between the two functions was 162° (Figure 14).

Indications of hair replacement in spring are:

- the small dip in the number of growing hairs per unit area in March 1975 and the increase in the number of growing hairs in May 1975
- the decrease in the number of non-medullated hairs from about 110 hairs

per 20 mm^2 in March 1975 to about 10 hairs per 20 mm^2 in May 1975

- the increase in the number of medullated hairs from about 150 per 20 mm^2 in March 1975 to about 230 per 20 mm^2 in May 1975.

The marked decrease in hair length during the winter months (Figure 10e) indicates that the longer hairs shed first.

The peak in the number of growing hairs per unit area in November 1975 indicates that new hairs appeared in the coat at a great rate in autumn. Figures 13 and 14 show that in autumn the number of medullated hairs per unit area decreased, whereas the number of non-medullated hairs per unit area increased markedly. Towards autumn hair density also increased. Figure 10e shows that hair length increased in autumn from about 20 mm to about 40 mm. It seems hard to believe that this increase in hair length is brought about by new hairs growing so quickly.

These results do not answer the question whether the 'winter' coat is a completely new coat or mainly an elongation of the 'summer' coat.

To determine more exactly the nature of coat changes in autumn we bleached the coat at the midside area in 6 animals early in September 1976. The bleached hairs are referred to as the old hairs (present from the beginning of September). Hairs produced after the coat was bleached are referred to as the new hairs. Some results of measurements on hair coat samples of these 6 animals are shown in Figure 15. This Figure shows that the hair density increased from 320 hairs per 20 mm^2 in September and October 1976 to 370 hairs per 20 mm^2 in January 1977. For various characteristics Table 8 gives T-values for a test of the null hypothesis that the observations were a random sample. For the old hairs the alternative hypothesis was the presence of trends downwards whereas for the new hairs and the length of the hairs the alternative hypothesis was the presence of trends upwards. The number of old medullated hairs, the number of old fragmentary medullated hairs, and the total number of old hairs showed significant trends downwards. Figure 15a shows that the decrease in the number of old hairs during the period September 1976–March 1977 (from 320 to 50 old hairs per 20 mm^2) was mainly due to the decrease in the number of medullated hairs. For the number of old non-medullated hairs randomness was not rejected. The number of new medullated hairs, new fragmentary medullated hairs, new non-medullated hairs, and the total number of new hairs showed significant trends upwards. The number of new hairs per 20 mm^2 increased from 11 in October 1976 to 235 in March 1977.

So the hair coats of the experimental animals became woollier in autumn, because only medullated and fragmentary medullated hairs were shed, whereas the new hairs consisted of medullated and fragmentary medullated hairs as well as non-medullated hairs.

Figure 15a shows that in September 1976 no changes occurred in coat composition, whereas during the following months new hairs appeared at a great rate. In January 1977 about 50% of the old hairs were shed.

Figure 15b gives the mean number of hairs entering the coat per day and the mean number of hairs disappearing from the coat per day. This Figure shows

TABLE 8. T-values used to test against trends

Hair coat characteristics	T-values
Number of old hairs per 20 mm^2	–5.4***
Number of old med. hairs	–5.2***
Number of old frag. med. hairs	–5.1***
Number of old non-med. hairs	–1.6
Number of new hairs per 20 mm^2	4.6***
Number of new med. hairs	4.6***
Number of new frag. med. hairs	2.9***
Number of new non-med. hairs	3.9***
Length of old hairs	0.9
Length of new hairs	5.0***

*: $p < 0.05$
**: $p < 0.01$
***: $p < 0.005$

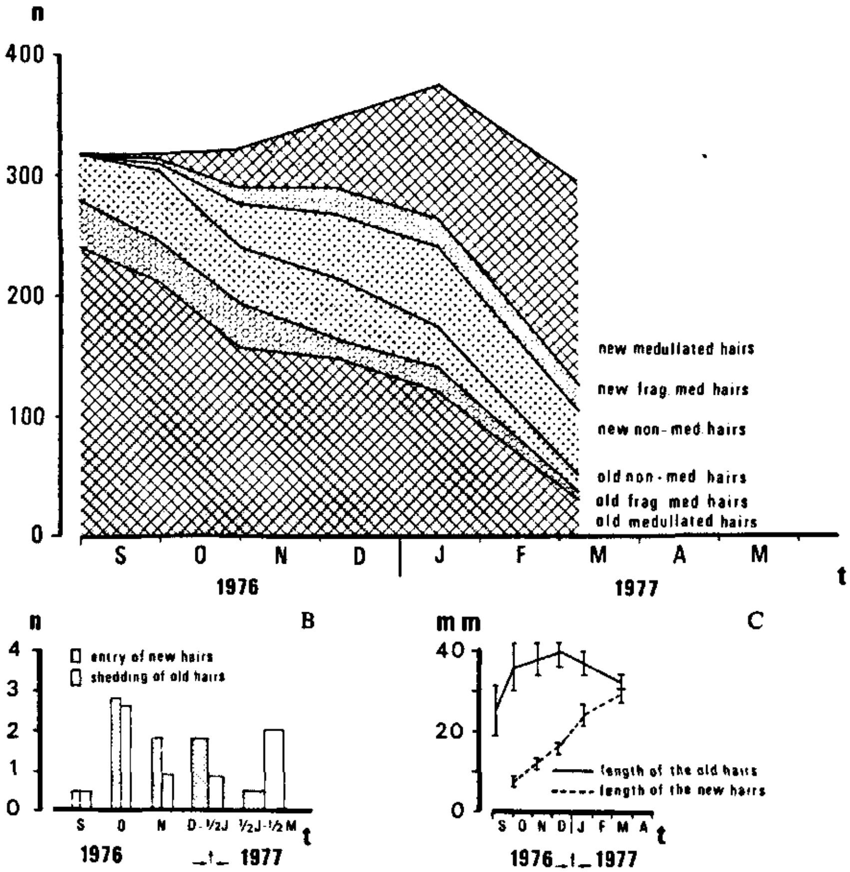


FIG. 15. Hair coat changes in 6 Friesian heifers, during the period September 1976–March 1977 A: hair coat composition per 20 mm^2 B: entry of new hairs per 20 mm^2 per day and shedding of old hairs per 20 mm^2 per day C: hair length

TABLE 9. F-values used in tests of significance of the multiple regression coefficients and the corresponding $R^2\%$ (percentage of the total variance) for the first five sampling dates

Sampling date	Body weight gain	Hair coat characteristics								
		All		Perc. of[a] med. hairs	Diameter of med. hairs	Diameter of frag. med. + non. med. h.	Hair lenght	Hair[b] density	Perc. of[a] anagen hair roots	Melanin[b] content
		F	R^2							
January	preceeding[c]	0.85	24							
	succeding[d]	0.42	11							
March	preceeding	2.07	45							
	succeeding	0.70	21							
May	preceeding	0.47	18							
	succeeding	2.60*	42							***
July	preceeding	2.60*	43							**
	succeeding	0.71	21							
September	preceeding	1.08	41							*

*: $p < 0.05$
**: $p < 0.01$
***: $p < 0.005$
a: arcsin $\sqrt{\%}$ transformation
b: logarithmic transformation
c: body weight gain during 2 months before the hair coat sampling date
d: body weight gain during 2 months after the hair coat sampling date

a peak of 2.7 new hairs per 20 mm^2 per day in October 1976; minima of 0.5 new hairs per 20 mm^2 per day occurred in September 1976 and during the period mid January-mid March 1977. The number of hairs that were shed was highest in October: 2.6 per 20 mm^2 per day. During the period mid January - mid March 1977 a large number of hairs was also shed: 2.1 per 20 mm^2 per day.

Figure 15c shows the changes in hair length during the period September 1976-March 1977. The large increase in hair length in September is striking. In November the old hairs ceased growing. The new hairs continued to grow until the end of the experiment. Figure 15c indicates that the increase in hair length in autumn resulted from the growth of hairs that were produced before early September.

3.2.3.5. Relationships between body weight gain and some hair coat characteristics

For the first five sampling dates multiple regression analysis was employed to determine the relationships between body weight gain and various hair coat characteristics. The results of the regression analyses are presented in Table 9. Percentage of fragmentary medullated hairs was not included in these analyses, because it is related to percentage of medullated hairs.

Only variation in body weight gain during the period May-July was significantly associated with variation in hair coat characteristics, both in May ($R^2 = 42$) and July ($R^2 = 43$). When the explained sum of squares was decomposed, it followed that only melanin content was significantly directly related to body weight gain. In September melanin content was also significantly related to body weight gain.

3.3. HAIR COAT CHARACTERISTICS IN FRIESIAN HEIFERS AFTER INTRODUCTION INTO KENYA

3.3.1. *Introduction*

This paragraph describes hair coat characteristics in Friesian heifers after introduction into Kenya. This study consisted of two parts: a preliminary study on heifers brought to Kenya in 1972 and a more extensive study on heifers brought to Kenya in 1973. The results we obtained deal with:

- variation in hair coat characteristics in heifers brought to Kenya in autumn 1972
- variation in hair coat characteristics in heifers brought to Kenya in autumn 1973
- shedding of the coat
- relationships between body weight gain and some hair coat characteristics.

3.3.2. *Material and Methods*

This section describes the material and methods used in this investigation. Appendix 7 gives a schematic presentation of the animals used, the sampling places, the sampling dates, and the measurements made on the hair coat samples.

3.3.2.1. Animals

From 1971-1973 about 2600 Friesian heifers were imported into Kenya. At the time of arrival in Kenya the ages of the animals ranged from 6 to 10 months. The heifers were reared on 2 government farms near Kitale, in North-West Kenya.

The animals used in the preliminary investigation were 30 Friesian heifers brought to Kitale in October 1972. These animals were a random sample from a batch of 1040 Friesian heifers exported to Kenya in autumn 1972. The 30 heifers were born between January 19th and April 23rd 1972. In the following pages these animals are referred to as the 1972-importation.

The main study was made on 32 Friesian heifers, a random sample from a batch of 519 Friesian heifers brought to Kitale in October 1973. These heifers were born between January 27th and April 25th 1973. In the following pages these animals are referred to as the 1973-importation. After November 1974 the number of animals in this main group fell steadily, because pregnant heifers were allocated to different farms all over Kenya.

3.3.2.2. Location and Climate

The animals of the 1973-importation were brought to the 'Katuke farm'. The animals of the 1972-importation were brought first to 'Broatch farm' and in 1973 also to 'Katuke farm'. Both farms are near Kitale, which is situated in latitude 1°N, longitude 25°E, and at an altitude of almost 2000 m.

According to the climatic classification of GRIFFITHS (1976) Kenya is situated in the Tropics in the climatic zone A2: hot, short dry spell (mean temperature of all months $\geqslant$ 18°C; rainfall 7-9 months each with $\geqslant$ 50 mm). Relief and altitude have a marked effect on the climate of Kenya. Conditions are very warm below 1000 m elevation and relatively cool above 2000 m.

Mean monthly temperatures, humidity, and precipitation for the 'Katuke farm' over the period November 1973-May 1975 are shown in Appendix 8.

Seasonal variation in temperature is slight; mean monthly temperatures varied from 19.5°C in July 1974 to 22.9°C in March 1975.

The wet season starts in March-April and ends in August, but some rain usually falls in September, October, and November.

Because of its position very close to the equator the seasonal variation in daylength in Kitale is only a matter of minutes.

3.3.2.3. Management

At Katuke farm the animals grazed on 550 hectares of natural pastures in paddocks of about 12 hectares. In the first two months after arrival the animals of the 1973-importation received 2 kg concentrates (a mixture of cottonseed cake, maizemeal, and sunflower bran)/head daily. The natural pastures provided very little feed in the dry season; the grass was poor in protein and high in fibre content. For instance, in December 1974 the chemical composition of some grass samples was estimated as containing 70.6% dry matter; 3.5% dry matter crude protein, and 39.1% dry matter crude fiber (GROOTENHUIS and PIETERSE, 1977). Therefore it was necessary to provide supplementary food in the dry season. The heifers of the 1973-importation received 10–15 kg maize silage or sorghum silage, 1 kg molasses-urea mixture, and 1 kg concentrates per head daily. During March–May 1974 (at the end of a dry season) and during October–December 1974 (at the beginning of a dry season) there was a shortage of silage, therefore during March and May 1974 and during October–December 1974 the heifers were fed on much less than 10 kg silage per day.

There are no figures on the supplementary food provided to the heifers of the 1972-importation.

The animals were dewormed regularly, and they were vaccinated against foot and mouth disease, rinderpest, and anthrax/black water.

Artificial insemination was used, the general aim being to start insemination at a weight of 340 kg. Pregnant heifers were allocated to different farms all over the country.

3.3.2.4. Measurements

Hair coat samples from the heifers of the 1972-importation were taken on the day of export in October 1972 and thereafter in April 1973 and October 1973.

Hair coat samples from the 32 heifers of the 1973-importation were taken on the day of export in October 1973 and thereafter at approximately regular intervals of three months until May 1975.

In most animals the samples were taken from the black area of the coat at the midside; unfortunately in 5 animals of the 1972-importation and in 3 animals of the 1973-importation the white area was sampled.

The methods used to measure hair coat characteristics are reported in paragraph 3.1. During the preliminary study the percentage of fragmentary medullated hairs, the melanin content, and the percentage of anagen hair roots were not measured.

The animals were weighed monthly at the same time of day.

3.3.2.5. Statistical procedures

Statistical analyses of the data on hair coat characteristics took the form of fitting curves by the method of orthogonal polynomials. This method is briefly described in 3.2.2.5.

Correlation coefficients between various hair coat characteristics were calculated per sampling date. Pooled correlation coefficients combining the correlation coefficients within sampling data were calculated using Fisher's z-transformation method (DE JONGE, 1963).

Multiple regression analysis was used to determine the relationship between body weight gain and various hair coat characteristics within each sampling date.

In order to use correlation and regression analyses it was necessary to transform the percentages of medullated hairs, fragmentary medullated hairs and anagen hair roots, and the data on hair density and melanin content, because their distributions were not normal. We transformed the hair density and melanin content data according to the equation Y = log x, in which Y = the transformed value and x = the original value. The percentage data were subjected to arcsin transformation. After these transformations the requirements to use classic methods were met.

3.3.3. *Results*

3.3.3.1. Variation in hair coat characteristics in heifers brought to Kenya in autumn 1972

In 5 of the 30 animals of the 1972-importation the white coat area was sampled. The data from these heifers had to be excluded from our calculations, for reasons given in 3.2.3.1.

Table 10 gives the polynomial regression analyses for the hair coat characteristics considered in this investigation. From the mean squares in Table 10 it appears that for diameter of medullated hairs and hair length both the combined linear regression term and the combined quadratic regression term proved significant. For diameter of fragmentary medullated plus non-medullated hairs and hair density the combined quadratic regression term was significant. Tests of the heterogeneity between the fitted polynomial regressions were based upon the ratios of heterogeneity mean squares and the remainder mean squares. These variance ratios proved insignificant. So there was no objection to using the combined analyses. In Figure 16 the regression lines are plotted graphically.

From the curves in Figure 16 the following can be ascertained:

- medullation

The curve for percentage of medullated hairs is a polynomial of degree zero, i.e. a constant (Figure 16a). So during the course of this experiment, the percentage of medullated hairs did not deviate from an average value of 40%. The percentage of fragmentary medullated hairs was not yet measured. Probably most of the fragmentary medullated hairs were classed with the non-medullated hairs.

- hair diameter

A second degree equation gave a good fit for the data on diameter of medullated hairs; the minimum occurred in May 1973 (Figure 16b). A second degree polynomial could be fitted to changes in diameter of non-medullated hairs, but the changes in this diameter were relatively small (Figure 16c).

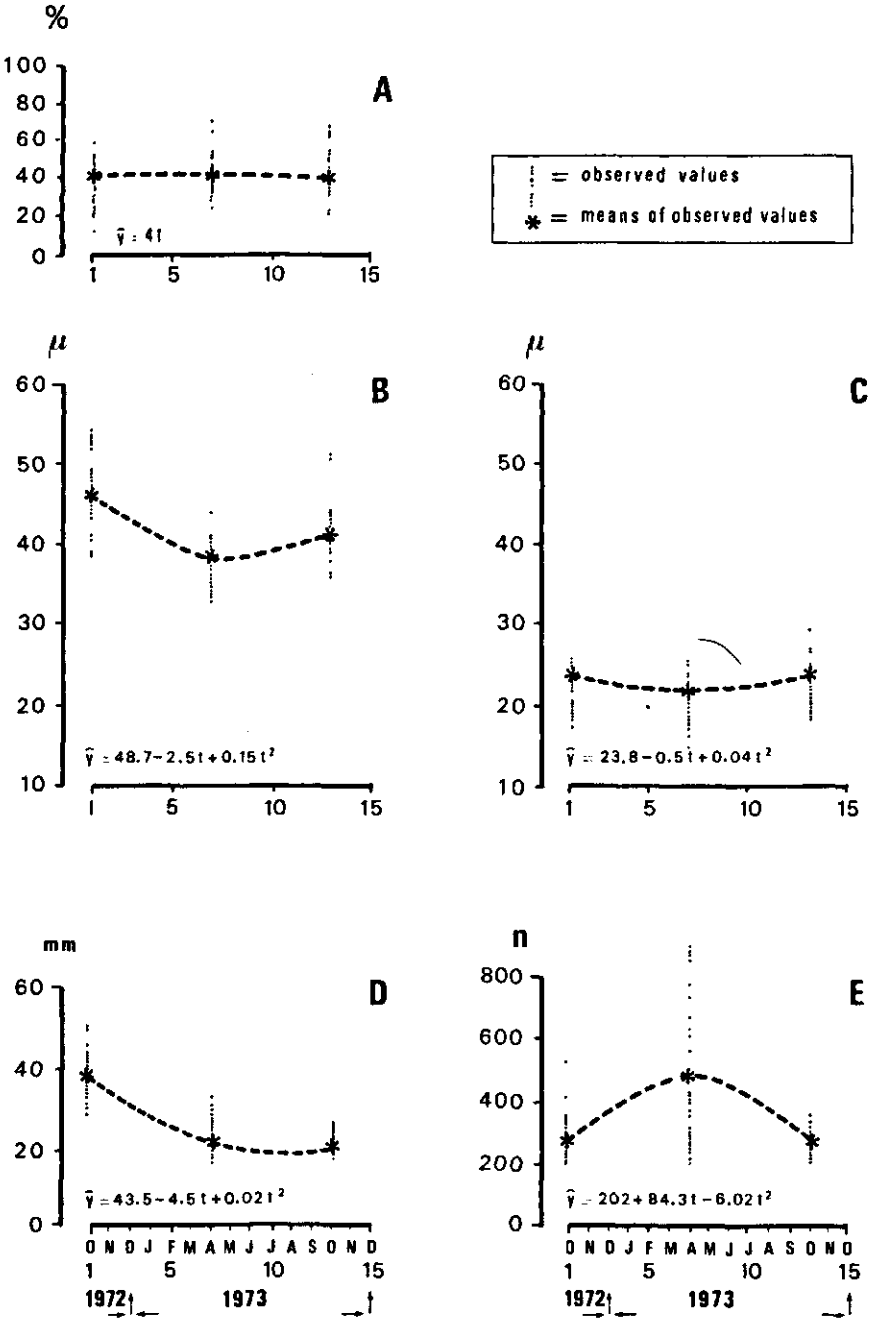


FIG. 16. Polynomial regression curves for 5 different hair coat characteristics from 25 Friesian heifers brought to Kitale in autumn 1972

A: percentage of medullated hairs
B: diameter of medullated hairs
C: diameter of non-medullated hairs
D: hair length
E: hair density per 20 mm^2

TABLE 10. Polynomial regression analyses for various hair coat characteristics in the heifers of the 1972-importation

Source of variation		Perc. of med. hairs			Diameter of med. hairs			Diameter of non-med. hairs			Hair lenght			Hair density		
		SS	df	MS	SS	df	MS	SS	df	MS	SS	df	MS	SS	df	MS
Linear	pooled	4596	24		490	24		120	24		3880	24		96874	24	
	combined	592	1	592	333	1	333***	0	1	0	3110	1	3110***	6821	1	6821
	heterogeneity	4004	23	175	157	23	7	120	23	5	770	23	33	90053	23	3915
Quadratic	pooled	3932	24		988	24		95	24		1468	24		907127	24	
	combined	176	1	176	513	1	513***	33	1	33*	1100	1	1100***	782359	1	782359***
	heterogeneity	3756	23	163	475	23	21	62	23	3	368	23	16	124768	23	5424
Remainder		4624	26	178	650	26	25	163	26	6	572	26	22	1427114	26	54889

*: $p < 0.05$
**: $p < 0.01$
***: $p < 0.005$
df: degrees of freedom
SS: sum of squares
MS: mean squares

- hair length

The curve for hair length decreases strongly from 40 mm in October 1972 to 20 mm in July 1973; thereafter the curve increases slowly (Figure 16d).

- hair density

The hair density curve increases progressively from an initial value of 280 hairs per 20 mm^2 to a peak of 500 hairs per 20 mm^2 in April 1973; thereafter the hair density decreased again (Figure 13e). The average hair density in April of 500 per 20 mm^2 is exceptionally high. The considerable variation in hair density in April between animals is also remarkable. Four heifers out of this group had a hair density of more than 800 hairs per 20 mm^2.

3.3.3.2. Variation in hair coat characteristics in heifers brought to Kenya in autumn 1973

Data on the characteristics of the hair coats of 3 of the 32 heifers of the 1973-importation had to be excluded from the calculations, because the white coat area was sampled.

On 16 heifers, hair coat sampling could not be continued until May 1975 because they were moved to different farms all over Kenya. On 27 heifers the sampling could be continued until February 1975; the data on the hair coat characteristics of these animals were included in the polynomial regression analyses (Table 11). For all characteristics considered in this study a polynomial regression line could be fitted through the group means. The heterogeneity mean squares show that the plotted regression lines are representative for all animals.

Figure 17 gives the graphical representation of the regression lines, and gives the results of measurements of hair coat characteristics from the 13 heifers that could be sampled until May 1975. These analyses led to the following being established:

- medullation

Polynomials to the second degree fitted changes in percentage of medullated hairs satisfactorily. The curve shows that the percentage of medullated hairs remained constant (at about 50%) for the first 12 months, but that from November 1974 it increased gradually (Figure 17a). In May 1975 the percentage of medullated hairs was about 80%.

Beginning in January 1974 the curve of the changes in percentage of fragmentary medullated hairs rises rapidly from an initial value of about 4% to

FIG. 17. Polynomial regression curves for 8 different hair coat characteristics from 27 Friesian heifers brought to Kitale in autumn 1973

A: percentage of medullated hairs
B: percentage of fragmentary medullated hairs
C: diameter of medullated hairs
D: diameter of fragmentary medullated plus non-medullated hairs
E: hair length
F: melanin content.
G: hair density per 20 mm^2
H: percentage of anagen hair roots

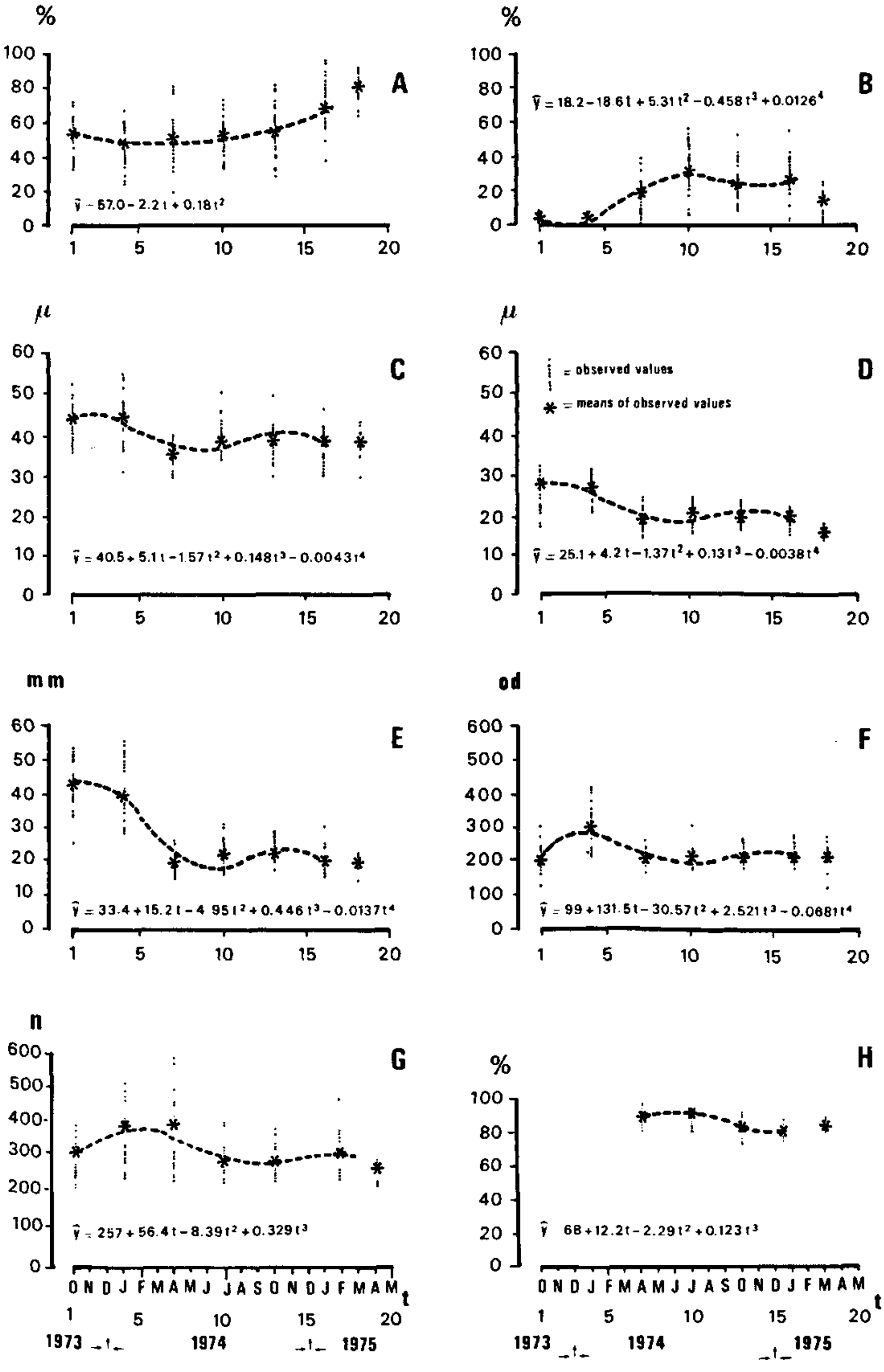

%
100
80
60
40
20
0
A
ŷ - 57.0 - 2.2 t + 0.18 t²
1
5
10
15
20
%
B
ŷ = 18.2 - 18.6 t + 5.31 t² - 0.458 t³ + 0.0126⁴
μ
60
50
40
30
20
10
C
ŷ = 40.5 + 5.1 t - 1.57 t² + 0.148 t³ - 0.0043 t⁴
μ
D
= observed values
= means of observed values
ŷ = 25.1 + 4.2 t - 1.37 t² + 0.13 t³ - 0.0038 t⁴
mm
E
ŷ = 33.4 + 15.2 t - 4 95 t² + 0.446 t³ - 0.0137 t⁴
od
600
500
400
300
200
100
F
ŷ = 99 + 131.5 t - 30.57 t² + 2.521 t³ - 0.0681 t⁴
n
G
ŷ = 257 + 56.4 t - 8.39 t² + 0.329 t³
O N D J F M A M J J A S O N D J F M A M
t
1973 → t ←
1974
→ t ← 1975
%
H
ŷ 68 + 12.2 t - 2.29 t² + 0.123 t³
O N D J F M A M J J A S O N D J F M A M
t
1973 → t ←
1974
→ t ← 1975

TABLE 11. Polynomial regression analyses for various hair coat characteristics in the heifers of the 1973-importation

Source of variation		Perc. of med. hairs			Perc. of frag. med. hairs			Diameter of med. hairs			Diameter of frag. med. plus non-med. hairs		
		SS	df	MS	SS	df	MS	SS	df	MS	SS	df	MS
Linear regression	pooled	6532	26		15884	26		1035	26		844	26	
	combined	2944	1	2944***	13484	1	13484***	473	1	473***	675	1	675***
	heterogeneity	3588	25	144	2400	25	96	562	25	23	169	25	7
Quadratic regression	pooled	4836	26		4032	26		327	26		405	26	
	combined	2532	1	2532***	1532	1	1532***	158	1	158*	180	1	180***
	heterogeneity	2304	25	92	2500	25	100	169	25	7	225	25	9
Cubic regression	pooled	2520	26		3540	26		338	26		483	26	
	combined	20	1	20	1040	1	1040***	10	1	10	20	1	20
	heterogeneity	2500	25	100	2500	25	100	328	25	113	463	25	18
Quartic regression	pooled	3252	26		3344	26		641	26		372	26	
	combined	152	1	152	2144***	1	2144	248	1	248***	203	1	203***
	heterogeneity	3100	25	124	1200	25	48	393	25	16	169	25	7
Remainder		19608	57	344	7524	57	132	1283	57	23	315	57	6

TABLE 11. (continued)

Source of variation		Hair length			Melanin content			Hair density			Perc. of anagen hair roots		
		SS	df	MS	SS	df	MS	SS	df	MS	SS	df	MS
Linear regression	pooled	10580	26		31303	26		193491	26		432	26	
	combined	10480	1	10480***	8403	1	8403	39166	1	39166*	267	1	267***
	heterogeneity	100	25	4	22900	25	916	154325	25	6173	165	25	7
Quadratic regression	pooled	2100	26		22057	26		277655	26		806	26	
	combined	1750	1	1750***	1907	1	1907	48855	1	48855*	560	1	560***
	heterogeneity	350	25	14	20150	25	806	228800	25	9152	246	25	10
Cubic regression	pooled	20	26		61088	26		224760	26		739	26	
	combined	10	1	10	39138	1	39138***	128010	1	128010***	735	1	735***
	heterogeneity	10	25	0.4	21950	25	878	96750	25	3870	4	25	0.2
Quartic regression	pooled	3040	26		82560	26		235610	26				
	combined	2540	1	2540***	50160	1	50160***	2500	1	2500			
	heterogeneity	500	25		32400	25	1296	233110	25	9324			
Remainder		2680	57	47	114456	57	2008	670263	57	11759	1663	29	57

*: $p < 0.05$	SS: sum of squares
**: $p < 0.01$	MS: mean squares
***: $p < 0.005$	df: degrees of freedom

a peak of even 30% fragmentary medullated hairs in August 1974 (Figure 17b).

– hair diameter

Both for diameter of medullated hairs and diameter of fragmentary medullated plus non-medullated hairs the combined linear, quadratic and quartic regression terms proved significant. The curve of the changes in diameter of medullated hairs indicates a steady decrease from December 1973 to June 1974; thereafter this diameter followed a smooth curve with a small peak in December 1974 (Figure 17c). The diameter of fragmentary medullated plus non-medullated hairs decreased steadily until June 1974; thereafter this diameter followed a smooth curve (similar to that of the diameter of medullated hairs), with a small peak in December 1974 (Figure 17d).

– hair length

First, second and fourth degree polynomials could be fitted to the changes in hair length. The shape of the graph for hair length shows a progressive decline in hair length in Kitale to about 50% of the maximum value. The minimum was recorded in July 1974 (Figure 17e).

– melanin content

A fourth degree equation gave a good description of the changes in melanin content during the course of our experiment. The curve peaked at 290 o.d. (optical density units per 50 mg of hair) in January 1974 (Figure 17f). From May 1974 the melanin content changed very little (about 200 o.d.).

– hair density

Second and third degree polynomials could be fitted to the changes in hair density. The most striking feature of the graph is the high hair density (about 390 hairs per 20 mm^2) in February–May 1974. After May 1974 a gradual decrease set in (Figure 17g). The considerable variation in hair density between animals in the samples from January and May 1974 is notable (January, standard deviation: 110 hairs per 20 mm^2; May, standard deviation: 150 hairs per 20 mm^2).

– percentage of anagen hair roots

From May 1974 the percentage of hair roots in anagen phase was measured. The combined linear, quadratic and cubic regression term proved significant. This percentage increased from 78% in May 1974 to 89% in August 1974; thereafter it remained at about 85% (Figure 17h).

Correlation coefficients between various hair coat characteristics

Table 12 gives pooled correlation coefficients between various hair coat characteristics for the first six sampling dates. In general the correlation coefficients were low. They showed that the diameter of fragmentary medullated hairs and non-medullated hairs was significantly positively ($p < 0.01$) correlated with hair length and with percentage of anagen hair roots, and negatively ($p < 0.05$) with percentage of medullated hairs. Highly significant positive correlation coefficients occurred for the relationships between diameter of medullated hairs on the one hand and the percentage of medullated hairs ($p < 0.01$), the percentage of fragmentary medullated hairs ($p < 0.01$),

TABLE 12. Pooled correlation coefficients between various hair coat characteristics

	Perc. of med.^{a} hairs	Perc. of frag.^{a} med. hairs	Diameter of med. hairs	Diameter of frag. med. + non - med. hairs	Hair length	Hair density^b	Perc. of^a anagen hair roots
Perc. of frag. med. hairs (144)	–						
Diameter of med. hairs (144)	0.19**	0.21**					
Diameter of frag. med. + non-med. hairs (144)	–0.17*	–	0.16				
Hair length (144)	0.06	0.16	0.27**	0.21**			
Hair density (144)	–0.39***	–	–0.13	–0.04	–0.04		
Perc. of anagen hair roots (96)	0.02	0.01	0.21**	0.21**	0.13	0.02	
Melanin content (144)	–0.11	0.01	–0.04	0.02	0.02	–0.03	0.15

The figures within brackets correspond to the degrees of freedom
*: $p < 0.05$
**: $p < 0.01$
***: $p < 0.005$
a: arcsin $\sqrt{\%}$ transformation
b: logarithmic transformation
–: the correlation coefficients differed significantly from each other

hair length ($p < 0.01$), and percentage of anagen hair roots ($p < 0.01$) on the other hand. A higher percentage of medullated hairs was associated with a lower hair density ($p < 0.005$).

3.3.3.3. Shedding of the coat

The low percentage of medullated hairs and the high hair density in the first months in Kenya indicate that the natural hair growth cycle was disrupted in the experimental heifers. To get a better insight in the changes in the hair coats of the heifers of the 1973-importation we combined the results of the measurements of hair density, and percentages of medullated hairs and fragmentary medullated hairs (Figure 18).

The changes in the number of medullated hairs per unit area were relatively small. The number of non-medullated hairs per unit area decreased gradually from 180 per 20 mm^2 in January 1974 to less than 10 per 20 mm^2 in March 1975. The number of fragmentary medullated hairs per unit area increased to about 90 per 20 mm^2 in Kenya. The high hair densities in the first six months were due to the high number of non-medullated hairs and the increase in the number of fragmentary medullated hairs in this period. Figure 18 gives no decisive answer on the question about the shedding events in the hair coats of the experimental animals. Figure 17e shows that hair length decreased rapidly during the first six months, indicating that the longer hairs (which are mostly medullated hairs) were shed during this period. The percentage of anagen hair roots was lowest in May 1974 (Figure 17h). Figure 19 gives the number of

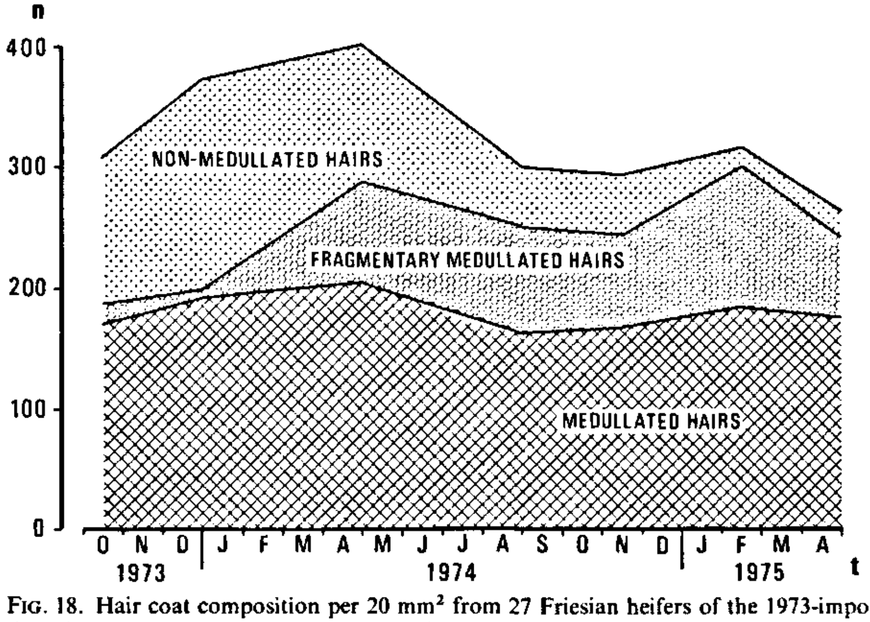
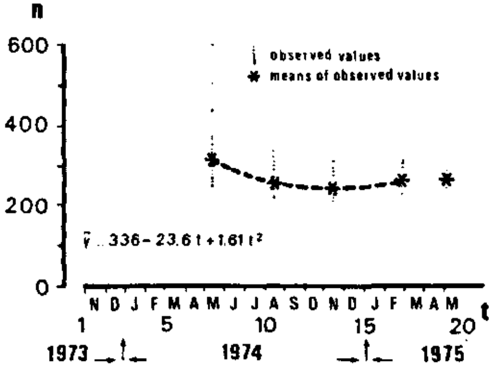


FIG. 18. Hair coat composition per 20 mm^2 from 27 Friesian heifers of the 1973-importation, during the period October 1973-April 1975

FIG. 19. Polynomial regression curve for the number of growing hairs per 20 mm²



growing hairs per unit area as a function of time. It was highest in May 1974. So both the number of growing hairs and the number of resting hairs per unit area were highest in May. From August 1974 to March 1975 the number of growing hairs per unit area remained almost constant. This suggests that during this period hairs were gradually replaced.

3.3.3.4. Relationships between body weight gain and some hair coat characteristics

Figure 20 gives the body weight curve of 27 heifers of the 1973-importation from their arrival at 'Katuke farm' up to March 1975. The figure shows that a satisfactory gain in body weight was maintained during most of this period. During March and May 1974 (end of a dry period), and October–December 1974 (beginning of a dry period) there was a shortage of silage. Figure 20 shows that the low plane of nutrition in these months affected body weight gain.

In the heifers of the 1973-importation for each sampling date multiple regression analyses were made to determine the relationships between preceeding and succeeding body weight gain and various hair coat characteristics. The results of the regression analyses are presented in Table 13. Percentage of

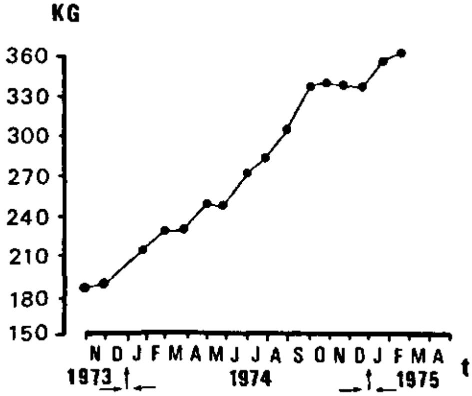


FIG. 20. Body weigth curve of 27 heifers of the 1973-importation from their arrival at Kitale up to March 1975

TABLE 13. F-values used in tests of significance of the multiple regression coefficients and the corresponding $R^2\%$ (percentage of the total variance)

Sampling date	Body weight gain	Hair coat characteristics								
		All		Perc. of[a] med. hairs	Diameter of med. hairs	Diameter of frag. med. + non. med. h.	Hair length	Hair[b] density	Perc. of anagen[a] hair roots	Melanin[b] content
		F	R^2							
October 1973	succeeding[c]	0.53	20							
January 1974	preceeding[d]	1.08	34							
	succeeding	0.55	21							
May	preceeding	6.79***	81	*			***			***
	succeeding	0.35	20							
August	preceeding	0.35	19							
	succeeding	0.64	30							
November	preceeding	2.85*	64	*						
	succeeding	2.41	40							
March 1975	preceeding	1.09	47							

*: $p < 0.05$
**: $p < 0.01$
***: $p < 0.005$
a: arcsin $\sqrt{\%}$ transformation
b: logarithmic transformation
c: body weight gain during 3 months before the hair coat sampling date
d: body weight gain during 3 months after the hair coat sampling date

fragmentary medullated hairs was not included in these analyses, because it is related to percentage of medullated hairs.

It is striking that the F-ratios for all hair coat characteristics were significant only in May 1974, and November 1974. During the period March–May 1974 81% of the variance in body weight gain was accounted for by the hair coat characteristics. When the multiple regression was decomposed it followed that melanin content, percentage of medullated hairs, and hair length were significantly directly related to body weight gain. In November the multiple regression accounted for 64% of the total variance in (preceeding) body weight gain. In this analysis the only significant coefficient was for the percentage of medullated hairs.

For the other sampling dates the percentages of variation (R^2) in body weight gain attributed to the various hair coat characteristics ranged from 20% to 47%, but the F-values were insignificant (Table 13). It must be emphasized that the degrees of freedom in these analyses were small.

4. DISCUSSION

4.1. INTRODUCTION

In this chapter the results from the experimental heifers in the Netherlands and from those taken to Kenya are discussed, compared as far as possible and (using data from the literature review) put in a physiological framework.

The data from the Netherlands on black and white hairs and on coat differences between body regions are discussed first. Then variations in hair coat characteristics in the experimental heifers in the Netherlands and in the experimental heifers brought to Kenya are described.

Most biological rhythms in animals appear to be stimulated by environmental events. The experimental heifers in the Netherlands were subjected to large seasonal changes in daylength and temperature, this in contrast with the heifers brought to Kenya. Because of its position in the vicinity of the equator and its altitude, in the area of Kitale there is only a slight variation in daylength and temperature during the year. So it was possible to make some remarks about the influences of photoperiod and temperature on hair coats. Relating live weight gain with nutrition also a suggestion about the influence of nutrition on hair coat changes could be put forward. Since this study was conducted under field conditions the effects of photoperiod, temperature, and also nutrition could not be separately assessed.

4.2. DIFFERENCES IN HAIR COAT CHARACTERISTICS BETWEEN BLACK AND WHITE COAT AREAS FROM THE MIDSIDE

KASSAB (1964) and BIANCA et al. (1974) sampled hair from Friesian cattle without considering the hair colour of the sampling sites. They did not take account of possible differences in hair coat characteristics between black and white hairs. However, Kassab (1964) found that between animals white hair samples were more medullated than black hair samples.

Our results showed that within animals, white hair fibres from the midside sampling area were more medullated than black hairs, and that mean diameters of white medullated hairs and of white fragmentary medullated plus non-medullated hairs were less than those of the corresponding black hairs. In 2.5.1. it was shown that medullation is directly related to the animal's ability to dissipate heat from the body. Furthermore white hairs absorb less solar radiation than black hairs.

It is remarkable that in the same animal there are differences between black and white hairs from the same sampling site. But although these differences cannot yet be explained it is clear that in comparative studies on hair coat characteristics, at least in Friesian cattle, black and white hairs must be regarded separately.

4.3. VARIATION IN HAIR COAT CHARACTERISTICS AT FOUR DIFFERENT BODY REGIONS

There is great variation in hair follicle characteristics over the body (see 2.2.7.). PAN (1964) and BIANCA et al. (1974) found that hair coat characteristics in cattle also varied between body regions. PAN (1964) based these findings on measurements on hair samples taken in autumn. BIANCA et al. (1974) worked with annual averages from different body regions. Cattle shed their coats in spring progressively along the body towards the tail dorso-ventrally (YEATES, 1955; HAYMAN and NAY, 1961). This suggests that the coat characteristics of different areas of the body need not remain constant during the year. This assumption was confirmed by our observations. In January percentage of medullated hairs, percentage of fragmentary medullated hairs, diameter of medullated hairs, diameter of fragmentary medullated plus non-medullated hairs, and hair density showed significant differences between body regions. But in July the coats of the experimental animals were uniform over the body. In November, however, percentage of medullated hairs, diameter of fragmentary medullated plus non-medullated hairs, and hair density again varied significantly over the 4 body regions. So results from studies on the variation in hair coat characteristics over different body regions made in one season cannot be extrapolated to other seasons.

In winter the high hair density in the shoulder area was notable. This is in agreement with the results obtained by FINDLAY and YANG (1950), HAFEZ et al. (1955), and PAN (1963), who found high hair follicle densities in this area. These authors found anterior-posteriorly increasing trends in hair follicle density. These trends are probably related to local skin tension. The low percentages of medulla in the belly and shoulder samples in winter were also striking. BIANCA et al. (1974) also found a low percentage of medullated hairs in the belly area and suggested that the correspondingly higher percentage of non-medullated hairs helped retain body heat.

When comparing coat characteristics of different animals the position chosen for measurements may be important. However, Figure 9 indicates that for most characteristics studied the variation over the body was much smaller than the seasonal variation.

4.4. VARIATIONS IN HAIR COAT CHARACTERISTICS IN THE EXPERIMENTAL HEIFERS IN THE NETHERLANDS AND IN THE EXPERIMENTAL HEIFERS BROUGHT TO KENYA

The pooled polynomial regression analyses yielded for each individual animal the mean, linear, quadratic, cubic and quartic coefficients of the polynomial curve, each of which represents some aspects of the changes in a characteristic in time. Table 14 gives the results of the estimations of the mean, linear, quadratic and cubic polynomial coefficients for both the experimental

TABLE 14. Means and standard deviations of the polynomial coefficients for the experimental heifers in the Netherlands (n = 30) and the experimental heifers of the 1973-importation (n = 27).

Hair coat characteristics		Polynomial coefficients							
		A		B		C		D	
		mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.
Perc. of med. hairs	The Netherlands	67.1	6.8	–	–	–2.9	0.7	0.3	0.1
	Kenya	56.8	9.6	1.3	1.7	0.9	1.3	–	–
	The Netherlands versus Kenya	***				***	**		
Perc. of frag. med., hairs	The Netherlands	10.4	3.1	0.1	0.03	–	–	–	–
	Kenya	18.4	5.4	2.7	1.2	–	–	–	–
	The Netherlands versus Kenya	***	**	***	***				
Diameter of med. hairs μ	The Netherlands	45.7	1.9	0.5	0.2	–	–	0.3	0.3
	Kenya	40.7	2.1	–0.6	0.5	0.2	0.3	0.1	0.3
	The Netherlands versus Kenya	***		***					
Diameter of frag. med. plus, non-med. hairs μ	The Netherlands	21.8	2.4	–	–	0.2	0.2	–	–
	Kenya	24.1	1.3	–0.1	0.03	0.3	0.3	–	–
	The Netherlands versus Kenya	***	**						
Hair length mm	The Netherlands	27.6	2.0	0.1	0.2	–	–	–0.9	0.2
	Kenya	29.1	3.7	–2.5	0.8	0.9	0.3	–	–
	The Netherlands versus Kenya	**	**	***	***				
Melanin content o.d.	The Netherlands	260	32	–0.4	0.2	12.9	3.5	–	–
	Kenya	228	25	–2.4	3.8	–	–	3.3	2.4
	The Netherlands versus Kenya	**			***				
Hair density per 20 mm²	The Netherlands	296	24	2.5	4.4	2.1	4.1	–2.3	2.8
	Kenya	330	36	–4.9	8.7	–4.4	10.1	5.0	0.5
	The Netherlands versus Kenya	**	*	**	**		***	***	***

* : $p < 0.05$	A: average	– polynomial coefficients showed no significance.
** : $p < 0.01$	B: linear term	The quartic terms are not included in this table.
***: $p < 0.005$	C: quadratic term	
s.d.: standard deviation	D: cubic term	

TABLE 15. Correlation coefficients between the polynomial coefficients for the experimental heifers in the Netherlands ($n = 30$) and the experimental heifers of the 1973-importation ($n = 27$)

Hair coat characteristics			Correlation coefficients		
			B	C	D
Percentage of med. hairs	The Netherlands	A	–	–0.11	–0.07
	Kenya	A	0.46*	–0.28	–
	The Netherlands versus Kenya				
Perc. of frag. med. hairs	The Netherlands	A	–0.04	–	–
	Kenya	A	0.68***	–	–
	The Netherlands versus Kenya		***		
Diameter of med. hairs	The Netherlands	A	–0.15	–	–0.01
	Kenya	A	–0.12	–0.16	0.12
	The Netherlands versus Kenya				
Diameter of frag. med. plus non-med. hairs	The Netherlands	A	–	0.02	–
	Kenya	A	–0.70***	0.43*	–
	The Netherlands versus Kenya				
Hair length	The Netherlands	A	0.01	–	–0.14
	Kenya	A	–0.76***	0.51***	–
	The Netherlands versus Kenya		***		
Melanin content	The Netherlands	A	–0.08	0.69***	–
	Kenya	A	–0.62***	–	0.43*
	The Netherlands versus Kenya		**		
Hair density	The Netherlands	A	–0.14	–0.04	–0.01
	Kenya	A	–0.24	–0.31	0.28
	The Netherlands versus Kenya				

*   : $p < 0.05$
** : $p < 0.01$
***: $p < 0.005$

A: average
B: linear term
C: quadratic term
D: cubic term

heifers in the Netherlands and the heifers of the 1973-importation. This table indicates clearly that for all characteristics the experimental heifers in the Netherlands followed a different regression pattern from the heifers of the 1973-importation. The relations between the linear, quadratic and cubic hair coat characteristic curve components, and the level were measured by correlation coefficients (Table 15). This table shows that another difference between the two groups was that in the Netherlands the changes in almost all characteristics were of the same magnitude whatever the level, whereas in Kenya the magnitude of changes in percentage of medullated hairs, percentage of fragmentary medullated hairs, diameter of fragmentary medullated plus non-medullated hairs, hair length and melanin content correlated with the level for the characteristic concerned.

An impression of the variations in the hair coat characteristics in the experimental heifers in the Netherlands and in the experimental heifers brought to Kenya can be read directly from the graphs in the Figures 10, 16 and 17. For medullation, hair diameter, hair length, melanin content and hair density these variations are discussed under the appropriate headings.

In the Netherlands twelve heifers were the progeny of Dutch Friesian bulls and eighteen heifers were the progeny of British Friesian bulls. The question arises whether this could have influenced the results. Our experimental plan was not suited to answer this question completely. However, for all hair coat characteristics considered the differences in the polynomial coefficients between the two groups were found to be insignificant.

4.4.1. *Medullation*

In the experimental heifers in the Netherlands the changes in percentage of medullated hairs were bell-shaped. There was a peak of about 90% in the summer months with corresponding dips during the winter months of about 50%. The changes occurred with little variation in all animals, regardless of the actual level of percentage of medullated hairs. KASSAB (1964) found that the percentage of medullated hairs in a small number of Friesian cows in the Netherlands varied from 64% in winter to 100% in summer. In Switzerland, BIANCA et al. (1974) found the percentage of fibres showing medullation in four Friesian heifers was only 30%. But this last figure was an annual average for the shoulder area. The difference in sampling positions probably accounts for at least some of the difference between the results obtained by BIANCA et al. (1974) and the results from the Netherlands, as in winter we found a much lower percentage of medullated hairs in the shoulder area than in the midside area. Our values for percentage of medullated hairs are comparable to percentages of medullated hairs reported for Jersey, *Bos indicus*, and *Bos indicus* × *Bos taurus* cattle in Australia (Appendix 3). However, British beef cattle had coats with a much lower percentage of medullated hairs. In rough-coated Shorthorns in Queensland in autumn and winter the coat consisted even almost entirely of non-medullated hairs (DOWLING, 1956 and 1959) (Appendix 3). Contrary to the literature we did not include fragmentary medullated hairs in our data about percentages of medullated hairs. If we had included fragmentary medullated hairs in our data about percentages of medullated hairs the differences between our data and the data collected by BIANCA et al. (1974) and by the Australian workers on British beef animals would have been greater. However, the percentages of fragmentary medullated hairs were low during the period investigated. No results for this characteristics are known from the literature. Fragmentary medullated hairs show much more resemblance with non-medullated hairs than with medullated hairs. Therefore it is not justified to classify hairs solely on the presence or absence of medulla.

During the course of the experiment with the heifers brought to Kenya in autumn 1972, the percentage of medullated hairs did not deviate from an average value of 40%. In the heifers of the 1973-importation the percentage of medullated hairs also remained constant (at about 50%) for the first 12 months. This percentage was comparable to the percentage of medullated hairs in the winter months found in the experimental heifers in the Netherlands. From November 1974 it increased gradually. In May 1975 about 80% of fibres showed medullation. Unfortunately it was impossible to continue the sampling after this date, because most animals had been taken to farms all over Kenya. In the Netherlands the changes in percentage of medullated hairs coincided with the changes in daylength. Probably the equatorial photoperiod has disturbed the changes in this characteristic in the heifers brought to Kenya.

In the heifers of the 1973-importation the percentage of fragmentary medullated hairs rose markedly. A peak of about 30% was recorded in August 1974. Under the heading 'hair density' (4.4.5.) I will return to this increase.

4.4.2. *Hair diameter*

In the experimental heifers in the Netherlands the diameter of medullated hairs increased steadily. It was significantly ($p < 0.005$) higher in the second winter (January–March 1975) than in the first winter (January–March 1974). This could have been due to increasing age of the animals. KASSAB (1964) found that hair diameters of calves were smaller than those of their dams.

The mean diameter of the medullated hairs was 46 μ and that of the fragmentary medullated plus non-medullated hairs was only 25 μ. PAN (1964) also measured diameters of medullated hairs and non-medullated hairs. He found a much smaller difference in mean diameter between these categories: in Jersey cows the mean diameter of medullated hairs was 54 μ and that of non-medullated hairs 41 μ. It must be emphasized that in our investigation the estimate of the mean diameter of medullated hairs was based on measurements on almost fully medullated hairs, and that the fragmentary medullated hairs, were combined with the non-medullated hairs to give an estimate of the mean diameter of these hairs.

Mean diameters of all hairs ranged from 33 μ in January and March 1974 to 44 μ in September 1974. These values agreed with the mean hair follicle diameters (41–53 μ) and mean hair diameters (38–50 μ) obtained by NAY and JOHNSON (1967), JENKINSON and NAY (1968) and BIANCA et al. (1974) in Friesian cattle (Appendices 1 and 4). KASSAB (1964) and BERMAN and VOLCANI (1961) found much higher diameters (56–103 μ) in Friesian cattle. BERMAN and VOLCANI (1961) determined hair diameters on the thigh area, BIANCA et al. (1974) on the shoulder area, and the other investigators on the midside area. These differences in sampling positions probably account for at least some of the differences between the mean hair diameters.

In the heifers of the 1972-importation mean diameters of all hairs ranged from 32 μ in October 1972 (on the day of export) to 28 μ in April 1973. In the heifers of the 1973-importation the mean diameter of all hairs dropped from 37 μ in October 1973 to 29 μ in May 1974. In both groups the diameter of medullated hairs decreased steadily during the first six months in Kenya.

The average diameter of medullated hairs was significantly ($p < 0.001$) lower in the experimental heifers of the 1973-importation than in the experimental heifers in the Netherlands (46 μ versus 41 μ) (Table 14).

Differences in fibre diameter result from differences in the amount of germinative tissue within the follicle bulb (HENDERSON, 1965). In sheep it has been found that diet affects the amount of germinative tissue. It is possible that the lower nutritional status of the heifers in Kenya has caused the decrease in hair diameters. In 4.7.3. I will return to the relation hair diameter–nutrition.

4.4.3. *Hair length*

The trends in hair length in the experimental animals in the Netherlands are in general agreement with those reported in the literature: a gradual decrease from winter to summer and a strong increase from summer to late autumn. The changes in hair length occurred with little variation in all animals. Precise comparisons of our data with data found in the literature are difficult, because of differences in the methods of measuring hair length.

It has been found that hair follicles are longer and deeper in winter than in summer (NAY and HAYMAN, 1963; JENKINSON et al., 1975). And HENDERSON (1965) has found that in the same animal the follicle length is related to the fibre length. So the shorter the follicle, the shorter on the whole is the hair produced. And it is interesting to note the assumption of JENKINSON et al. (1975) that short hair follicles can be regarded as an adaptation to warm environments.

In the heifers of the 1972- and 1973-importations the hair length decreased rapidly during the first six months to about 50% of the values on the day of export and levelled off later in all animals. At the time of first sampling, on the day of export, the hair length of these heifers was the same as the hair length of the experimental heifers in the Netherlands in late autumn. After a few months in Kenya the hair length of the heifers of the 1972- and 1973-importations was approximately the same as that of the experimental heifers in the Netherlands in spring and summer.

In 2.5.4. it has been assumed that ambient temperature is inversely related to hair length and that the thyroid probably controls the effect of temperature on hair growth. This is discussed further in section 4.7.2.

4.4.4. *Melanin content*

BERMAN (1960) has established that thyroxine also stimulates hair pigmentation. He found that the amount of hair pigment is greatest during the winter. Our results support this: the melanin content was much higher in winter months than in summer. The melanin content started to increase in late autumn. On the other hand in Queensland SCHLEGER (1962) found that in calves and lactating cows the colour score (determined by visual observations) was higher in summer coats than in winter coats, however, the differences were rather small. This discrepancy with our results can be explained by the fact that in summer hairs are much more medullated than in winter, and the thicker medullated hairs tend to appear darker than fine hairs. The large intra- and intercellular air spaces in the medulla greatly affect the colour tones of the hairs.

In the hair samples from the heifers of the 1973-importation the melanin content increased slightly from November 1973 to January 1974 (possibly still a reaction to the seasonal cycle of the Netherlands), but thereafter the melanin content decreased again. On the whole the melanin content hardly varied during the period investigated and was about the same as that of the experimental heifers in the Netherlands in summer.

4.4.5. *Hair density*

In the literature it has generally been assumed that both the follicles per unit area of skin and the number of hairs decrease as the animal grows (DOWLING, 1959; BIANCA et al., 1974), and that in cattle hair density is not subject to seasonal changes. This being the case it should be possible for the same follicle to produce a medullated hair at one time and a non-medullated hair at another time. A change from a medulla-producing follicle to a follicle producing a non-medullated fibre will require quite a reorganization of cells within the bulb, as medulla-producing follicles have much larger bulbs and papillae compared to follicles producing non-medullated fibres. Furthermore their papillae occupy a larger proportion of their bulb volumes (HENDERSON, 1965; STRAILE, 1965). Contrary to the assumption in the literature, in the experimental heifers in the Netherlands, and in the experimental heifers of the 1972- and 1973-importations, the expected gradual decrease in hair numbers per unit area of skin did not occur.

To compare our results with literature hair density figures are given in numbers per cm^2. The hair density in the experimental heifers in the Netherlands decreased gradually from about 1550 hairs per cm^2 in January 1974 to about 1350 hairs per cm^2 in summer, but towards autumn hair density increased again, reaching a peak of 1650 hairs per cm^2 in late autumn. There was no decrease from January 1974 to January 1975. The slopes of the polynomial lines were found to differ significantly between the heifers (Table 6). This heterogeneity may partly be caused by our method of measuring hair density, because the determination is relatively crude. In the 6 heifers used in the shedding experiment, the hair density also increased in autumn (from about 1600 per m^2 to 1850 per cm^2). BIANCA et al. found an annual average of 1455 hairs per cm^2 in Friesian heifers. Follicle densities in mature Friesians reported in the literature range from 791 to 1517 per cm^2 (Appendix 2).

In the heifers of the 1973-importation the hair density increased rapidly during the first months in Kenya: from about 1500 hairs per cm^2 to about 2000 hairs per cm^2. After May 1974 a decrease set in. There was a considerable variation in hair density between animals in the samples from January 1974 and May 1974. In the heifers brought to Kenya in autumn 1972 the hair density increased progressively from 1400 hairs per cm^2 to a peak of as much as 2500 hairs per cm^2 in April 1973: thereafter the hair density decreased again to 'normal' values. Our results cast doubts on the assumption made by HAYMAN and NAY (1961) that follicle population figures are equivalent to hair population figures.

Several causes can be suggested to explain the extremely high hair densities found in some animals in Kenya:

- two hairs growing from one follicle

Normally a club hair is held in the follicle until the papilla has started to produce a new hair. When a follicle grows two hairs, the club hair does not fall out and the new hair grows alongside it. There are no reports in the literature indicating that this occurs in domestic animals. At our laboratory, however, skin samples from 15 Friesian heifers brought to Tunisia showed that in 2 animals a number of follicles (about 10%) contained 2 hairs. These animals also had a high hair density (BOSMA and JANSEN, 1977).

- a great number of 'loose' hairs

How far 'loose' hairs have influenced our density data is not clear. However, in Friesian cows in Israel the percentage of 'loose' hairs in the coat was found to be only about 3% (BERMAN and VOLCANI, 1961).

- errors arising from sampling method.

We have no evidence that one or more of these suggestions explain the extremely high hair densities found in some animals during the first months in Kenya.

The seasonal changes in hair density in the Netherlands indicate that in spring and summer there are more empty follicles than in autumn and winter. This could be because a number of follicles producing non-medullated hairs in autumn shed their hair in spring and remain empty in the summer months. So when there are fewer non-medullated hairs per unit area, there are probably more empty follicles per unit area. This hypothesis is supported by the observations that in comparison to summer coats of the heifers in the Netherlands, the coats of the heifers in Kenya contained many more non-medullated hairs, especially in the first six months in Kenya. In the heifers of the 1973-importation correlations between various hair coat characteristics indicated that a dense hair coat tended to be composed of more non-medullated hairs.

The number of medullated hairs in the heifers in the Netherlands varied from 750 to 1350 per cm^2. In the heifers of the 1973-importation the number of medullated hairs only varied between 850 to 1100 per cm^2. The number of fragmentary medullated hairs per unit area in the heifers of the 1973-importation varied from 400 to 450 per cm^2 during the period May 1974–March 1975. In the experimental heifers in the Netherlands the number of fragmentary medullated hairs varied from 65 to 220 per cm^2. These figures suggest that it is possible that in the heifers in Kenya a number of follicles were unable to grow a fully medullated hair. A possible explanation is the stress put on to the heifers adjusting themselves to a very different environment, especially with regard to the equatorial photoperiod (in the Netherlands the changes in the number of medullated hairs per unit area coincided with the changes in day-length) and to some extent with regard to the somewhat lower nutritional status of the heifers in Kenya (a large medulla-producing follicle needs more nutrients than a small follicle producing a non-medullated or a fragmentary medullated hair). This explanation is, however, purely speculative.

4.5. SHEDDING OF THE COAT

As was pointed out in paragraph 2.4. little agreement exists between authors on the shedding of the coat in cattle. According to YEATES (1954 and 1955) the winter coat is an elongation of the summer coat and shedding occurs only in spring. This does not explain why the coat becomes more 'woolly' in autumn and winter. DOWLING and NAY (1960), HAYMAN and NAY (1961), and TURNER and SCHLEGER (1970) found that most follicles grow two hairs in a year and they concluded that the winter coat is a completely new coat. But in autumn hair length increases markedly and it is difficult to understand how new hairs can grow so quickly.

Figure 12 shows that in the experimental heifers in the Netherlands there was a very high percentage of hair roots in the anagen phase during the course of the experiment. But as the hair density changed with season, the number of growing hairs per unit area also varied, with an increase in May and a large peak in November. These results agree with DOWLING and NAY (1960), HAYMAN and NAY (1961), and TURNER and SCHLEGER (1970), all of whom found a peak of about 70% of active follicles in autumn and a second lower peak in spring. Figure 14 shows both the changes in the number of medullated hairs per unit area and in the number of non-medullated hairs per unit area were bell-shaped. The phase difference between the two functions was 5.5. months. The sine functions illustrate well the changes in the hair coats of these animals and show that both in spring and in autumn large changes occur in coat composition. However, no information is available as to whether the winter coat is a completely new coat or not.

In an attempt to throw light on the conflicting opinions concerning the changes in the coat in autumn, we bleached the coat at the midside area in 6 animals early in September 1976. In the 6 animals used in the shedding experiment, new hairs appeared at a great rate from the beginning of October to mid January. The rate of entry of new hairs and the rate of shedding of old hairs were both highest in October. From October to January the rate of entry of new hairs (14 to 9 hairs per cm^2 per day) was higher than the rate of shedding of old hairs (13 to 5 hairs per cm^2 per day). The figures on the rate of entry of new hairs agreed broadly with results on this characteristic, obtained by TURNER and SCHLEGER (1970). In January the coats of these 6 animals consisted of equal numbers of old hairs and new hairs (Figure 15a). In March 83% of the old hairs were shed.

The coats of these animals became woollier in autumn because only a proportion of the medullated and fragmentary medullated hairs were shed, whereas the new hairs consisted of medullated, fragmentary medullated, and also non-medullated hairs. From mid January to mid March the hair density decreased because a large number of hairs was shed, whereas only a few new hairs appeared in the coat. The increase in hair length in autumn resulted from the growth of hairs that were produced before early September. From January the hair length decreased. In the main group of 30 heifers the hair density, the hair length and the number of growing hairs per unit area also decreased in the winter. So one can infer that the longer hairs are shed first in winter.

Our results do not agree with the theories in the literature on the shedding of the coat. Probably the sequence of events in temperate zones is as follows:

- in spring most of the hairs are replaced, the non-medullated hairs disappear almost entirely from the coat and the new hairs are almost all medullated hairs
- in autumn about 50% of the hairs are replaced, non-medullated hairs appear in the coat again, and the increase in coat length results from the growth of the 'summer' hairs
- the increase in hair density in autumn is probably due to the fact that a number of follicles producing non-medullated hairs in autumn remain empty in the summer months
- under housed conditions the longer hairs are shed already in winter.
- some shedding of hairs takes place gradually throughout the year.

In the experimental heifers brought to Kenya the longer hairs (which are mostly medullated hairs) were shed during the first six months. But the hair density increased markedly in this period. The high hair density in the first six months in the heifers of the 1973-importation was probably caused by:

1) the fact that the non-medullated hairs were shed only very gradually; it took about 17 months to reduce the number of non-medullated hairs to less than 50 per cm^2, whereas in the Netherlands in spring it took only a few months to reduce the number of non-medullated hairs per unit area to less than 50 per cm^2
2) the high number of fragmentary medullated hairs that appeared in the coat.

From August 1974 the hairs were gradually replaced. Unfortunately we did not dye the hair coat to determine the nature of the hair replacement in Kenya.

It is not understood what factors are responsible for the fact that the non-medullated hairs remained in the coat for such a long time. As it is known that shedding of the coat is initiated by changes in the photoperiod, it is possible that the equatorial photoperiod was involved. It is also possible that the somewhat lower nutritional status of the heifers in Kenya has delayed the shedding of the non-medullated hairs. However, only during a few months the nutritional conditions were really poor.

4.6. RELATIONSHIPS BETWEEN BODY WEIGHT GAIN AND SOME HAIR COAT CHARACTERISTICS

As was pointed out in paragraph 2.5., at high temperatures coat type has been found to be related to productivity not only indirectly by its influence on the efficiency of temperature regulation, but also directly as an indicator of an animal's condition (even in the absence of heat stress). There is no information from temperate zones about the relations between coat characteristics and performance.

In the experimental heifers in the Netherlands multiple regression analysis was used on the data from the first 5 sampling dates to determine relations between body weight gain and various hair coat characteristics. Only the melanin content of the hairs from the samples taken in May and July, and September were found to be significantly related to body weight gain respectively during the periods mid May–mid July and mid July–mid September. The biological significance of this relationship is not fully clear. In Queensland (Australia) SCHLEGER (1962) found that the intensity of the red colour in Herefords and Shorthorns and crosses between them and the Africander was directly correlated with body weight gain. Schleger suggested that the melanin content, the end-product of a series of enzymic processes, is an index of general enzymic activity. How far differences between high and dark shades of black hairs are of importance with regard to absorptivity is not known. RIEMERSCHMID and ELDER (1945) compared six coats of different shades of red, they found that the mean effective absorptivity varied only between 78 percent and 83 percent. SCHLEGER (1962) established that seasonal changes in the intensity of red colour in Herefords, Shorthorns, and crosses between these and the Africander had no influence on rectal and skin temperatures.

In the experimental heifers in the Netherlands the seasonal changes in most hair coat characteristics we studied occurred with little variation in all animals; therefore no relationship between hair coat characteristics and performance can be expected on the grounds of the influence of coat type on the efficiency of temperature regulation. Since this study was conducted under field conditions and, as these data have few degrees of freedom, relationships between hair coat characteristics and performance can be expected to be insignificant.

This last consideration also holds for the results from the multiple regression analyses for each sampling data in the heifers of the 1973-importation. Only the hair coat characteristic measurements of the hair samples taken in May 1974 and November 1974 were significantly related to body weight gain. During the period March–May 1974, 81% of the variance in body weight gain was accounted for by the hair coat characteristics. In November the multiple regression accounted for 64% of the total variance. Both in May and November the percentage of medullated hairs was significantly related to body weight gain. Melanin content was only in May related to body weight gain.

The discovery that in the very periods with rather a low plane of nutrition (dry periods) hair coat characteristics were significantly related to body weight gain, is of interest in relation to the conclusions reached by other authors that sleek, medullated hair coats indicate capacity to react favourable in the face of stress (SCHLEGER and TURNER, 1960; TURNER, 1962).

4.7. ENVIRONMENTAL INFLUENCES

4.7.1. *Photoperiod*

In the temperate regions seasonal variations in nature are so strong that most living beings have to follow them. The seasonal changes in hair coat help the animal to preserve thermoneutrality, therefore it has long been thought that they are regulated by environmental temperature. This speculation was easily disproved by YEATES (1954 and 1955), who found that coat shedding was influenced by changes in photoperiod regardless of the temperatures to which the animals were exposed. This is not surprising, for the seasonal variation in photoperiod is absolutely regular.

Figure 11 shows that sine curves described the seasonal changes in daylength and the average rhythm in percentage of medullated hairs (which represents the seasonal variation in coat type) very well. The sine functions indicated that the cycle of percentage of medullated hairs was closely related to changes in daylength but with a time lag of about 1 month. These results provide further evidence that variations in daylength regulate the hair growth cycle. Although the mechanism of the link photoperiod – hair growth cycle is not yet fully understood.

According to RYDER (1971) the photoperiod serves to 'set' the biological clock that controls the annual hair growth cycle. He maintains that especially the equinoxes are of importance in 'setting' the clock. In the heifers in the Netherlands large changes in coat composition occurred after the spring equinox and after the autumn equinox. According to PALMER (1976) no clock can be sensitive to temperature changes and still function as a timepiece, because if temperature does change the rate at which it runs it will no longer act as a clock, but instead will assume the characteristics of a thermometer. Almost nothing is known about the physiological mechanism of the 'clock' underlying seasonal rhythms and its synchronization by daylength.

In paragraph 2.1. it has been postulated that the thyroid has a stimulating effect on the hair growth and on the hair growth cycle and that adrenal cortex and gonadal hormones discourage the hair growth cycle. According to EBLING (1965) the changes in daylength act through the endocrine system on the hair growth cycle. According to FERGUSON et al. (1965) hormones may act on mitotic activity rate in the follicle bulb, on the growth of cells, or on the mobilization of specific limiting nutrients.

The heifers of the 1972- and 1973-importations were brought to Kenya in autumn. During the first 12 months in Kenya the percentage of medullated hairs remained at the same low level. The non-medullated hairs were shed only very gradually. And especially in the first six months these heifers grew very dense coats. Once the heifers were brought to Kenya they were no longer subjected to seasonal changes in daylength. And probably therefore in these heifers the rhythm in the composition of their coats did not persist. Perhaps the unchanging daylength disturbed the endocrine pattern of the temperate zone heifers.

4.7.2. *Temperature*

Seasonal modifications in nature do not result from any one environmental factor but probably from a complex interaction of various environmental effects with endogenous rhythms of the organism. The fact that changes in coat composition are under photoperiodic control does not exclude the possibility that temperature might also exercise some influence on hair growth.

In 2.4.3. it has been concluded that temperature can modify the seasonal loss of the winter coat. The decrease in hair length observed in the experimental heifers in the Netherlands in winter under housed conditions, and the decrease in hair length in the heifers in Kenya after a few months can be related to the shedding of the longer hairs. The influence of temperature especially on hair length has been discussed in 2.5.4. The influence of temperature may be mediated by the thyroid. In sheep it has been found that thyroxine acts especially on the size of follicle bulb cells (ROUGEOT, 1965).

As shown in 2.1.1.6. there is evidence that melanin production is hormonally controlled. In cattle thyroxine also stimulates hair pigmentation, and it is thought that temperature influences the melanin content (BERMAN, 1960). We found that melanin content was higher in the winter months than in summer. In Kenya the melanin content changed little during the period investigated.

4.7.3. *Nutrition*

In cattle the effect of nutrition on the hair coat has never been intensively investigated. In sheep it has been found that a poor diet reduces the diameter of fibres by reducing the effective germinative cell population in the follicle bulb (SHORT et al., 1965; RYDER, 1958; HENDERSON, 1965). During protein-calorie-malnutrition in man significant changes occur in the hair diameter (BRADFIELD, 1974). Over the period October 1974–May 1975 the experimental heifers in the Netherlands gained 98 (S.D.: 20) kg in body weight, whereas over the period October 1973–May 1974 the heifers of the 1973-importation gained only 56 (S.D.: 18) kg in body weight. The heifers of the 1972-importation gained 23 (S.D.: 26) kg body weight in the period January–May 1973. When we use these body weight gain data to indicate nutritional status, it may be suggested that the decrease in hair diameter in the first six months in Kenya is caused by the poorer nutritional status of the heifers in Kenya during this period.

In animals under very poor nutritional conditions the cycle of coat shedding and new hair growth is delayed (see 2.4.3. and 2.5.4.). Figure 20 shows that in the heifers of the 1973-importation a satisfactory gain in body weight was maintained during most of the period of our investigation. Research under controlled conditions is necessary to reveal the role of nutritional stress and other stresses on the hair coat.

4.8. CONCLUDING REMARKS

In the experimental heifers in the Netherlands in the summer the hairs were shorter, more medullated and therefore thicker, than in late autumn and winter, and the coat was also less dense owing to lack of non-medullated hairs. These changes may be regarded as seasonal acclimatization. Because as was shown in 2.5.1. insulation of the coat is inversely related to medullation and hair diameter, and directly related to hair length, coat depth and hair density. The characteristics of the summer coat allow greater efficiency of evaporative cooling.

We found also large seasonal changes in melanin content: it was much higher in winter than in summer. It is uncertain how far this is an adaptive character for heat regulation.

There is almost no quantitative information about the influence of hair coat characteristics on the heat transfer. In cattle only attention has been given to coat length to predict thermal insulation (GONZALEZ-JIMINEZ, 1962; BLAXTER and WAINMAN, 1964; WEBSTER et al., 1970). DAVIS and BIRKEBAK (1974) developed a complex theoretical model of fur (defined as the mixture of hair and air covering the body), to calculate the insulation of an animal's fur as a function of physical properties of the fur and hairs of the fur layer. We did not measure a number of the required characteristics (e.g.: the inclination of the hairs, the emissivity of the hairs, the thermal conductivity of the hairs) and therefore we could not apply this model. It is therefore not possible to relate our data to actual heat loss through the coat. In view of the data in 2.5.1. it can only be stated that in the heifers in Kenya the high hair densities, the low percentages of medullated hairs and the small hair diameters impeded heat dissipation. However, the decrease in hair length in the heifers was advantageous with regard to heat dissipation. Especially the extreme hair densities of about 4000 hairs per cm^2 in some animals in the first six months will have had an effect on heat exchange. Tregear (1965) showed that in a coat with a density of 1300 hairs per cm^2 the thermal conductivity was about twice as high as in a coat with a density of 4000 hairs per cm^2.

It is not exactly known under what kind of climatic conditions the coat will have implications with regard to heat dissipation. In hot dry climates in Australia animals with short, thick, medullated hairs have been found to tolerate heat much better and to have greater capacity to sweat than animals with woolly coats. In the climatic conditions of Kitale coat type may not be so important; mean temperatures ranged from 19.5 °C to 22.9 °C, mean monthly maximum temperatures were around 30 °C and mean monthly minima were around 11 °C. On only 2 of the six sampling dates was percentage of medullated hairs found to be significantly related to body weight gain. If the climate is more extreme (particularly in hot-wet climates) heat problems may arise in Friesians that are transferred from the temperate zone to equatorial regions. This needs further investigation.

The thermal insulation by the coat is a complex problem and laboratory research is necessary to reveal the role of various hair coat characteristics on heat transfer.

Various authors have drawn attention to the importance of the hair coat in determining the ability of an animal to adapt to their physical environment (see 2.5.3.). The dense hair coats in the first six months and the low percentages of medullated hairs in the first twelve months in the heifers of the 1972- and 1973-importations indicate that the hair coats of these heifers were out of phase with their physical environment during this period. There was a considerable variation between animals in the hair densities in the first 6 months. Thus the reaction to environmental conditions revealed by changes in density of medullated, fragmentary medullated and non-medullated hairs was much more variable in Kenya than in the Netherlands. The gradual increase in percentage of medullated hairs after 12 months suggests that after this period the hair coats of the experimental heifers adapted to their physical environment. In Kenya the magnitude of changes in most characteristics correlated with the level for the characteristics concerned.

As has been shown in paragraph 2.5.4. it is still an open question whether undesirable coat types depress adaptation to hot environments by interfering with heat loss from the skin, or whether these coats are outward signs of imbalance of internal functions related to the general physiological state of the animal. As was discussed above in a climatological environment such as Kitale the nature of the coat is probably not so important in relation to the thermal balance of the animal. Coat type as an indicator of susceptibility to stress will be of significance when animals and environment are out of harmony. The data showing that in Kenya in the very periods with rather a low plane of nutrition the percentage of medullated hairs was significantly related to body weight gain, agreed with other authors, that sleek medullated coats may be of significance as an index of well-adapted constitution (e.g. BONSMA, 1949; SCHLEGER and TURNER, 1960; TURNER, 1962). Because of the significance attached to coat type in hot climates there is need for more fundamental information to identify the environmental and physiological factors responsable for different animals growing different types of coat. Regarding environmental factors paragraph 4.7. is only a small contribution to this. In 2.5.4. it was concluded that endocrine functions and efficiency of energy metabolism are involved.

Evaluating the various hair coat characteristics it can be stated that medullation, hair length and hair density are useful characteristics to give a morphological description of seasonal hair coat changes. To determine the role of various stresses on the hair coat it is necessary to include hair diameter, hair replacement, and melanin content measurements.

5. SUMMARY

The export of about 2600 Friesian heifers to Kenya between 1971–1973 provided an opportunity of studying the adaptation problems experienced by these heifers. Within the framework of the NUFFIC (Netherlands Universities Foundation for International Cooperation) a research project entitled 'Adaptation of Dutch Friesian heifers in the Tropics, with special reference to Kenya' was initiated. This project studied aspects such as health parameters, reproduction and growth in the imported Friesians. Under the aegis of the project we studied the changes in cattle hair coat characteristics. This topic was chosen for 3 main reasons:

- The characteristics and the cyclic changes of the hair coat are important in the ecology of cattle.
- Various authors have drawn attention to the importance of hair coat type as an indicator of the ability of beef cattle to adapt to tropical climates.
- There were no data on adaptation problems, with regard to hair coats, of dairy cattle.

To complement the Kenyan data, I studied hair coat characteristics in Friesian heifers in the Netherlands. By thoroughly reviewing existing literature on hair follicles, sweat glands and hair coat characteristics in cattle, I obtained data that could be compared with the data I collected in Kenya and the Netherlands.

The literature review (Chapter 2.) comprises a résumé of the anatomy and physiology of the hair follicle and sweat gland (section 2.1.4.); a summary of hair follicle and sweat gland characteristics (section 2.2.12.), and hair coat characteristics of cattle (section 2.3.13.); a summary of coat shedding, the effects of photoperiod, temperature and nutrition (section 2.4.4.); and the major conclusions on how hair follicle, sweat gland and hair coat characteristics relate to heat exchange, performance and adaptation (section 2.5.5.).

Chapter 3 describes the experiments. The methods of measuring hair coat characteristics are given in paragraph 3.1. The hair samples were measured for medullation, hair diameter, hair length, melanin content, hair density and percentage of anagen hair roots. Our methods were generally the same as those reported in the literature, except for those we used to measure medullation and hair diameter.

The results of the research on hair coat characteristics of Friesian heifers in the Netherlands are described in 3.2. In this investigation 30 heifers were sampled at regular intervals. Supplementary observations on shedding of the coat were made on 6 heifers. We found that:

- In the same animal white hair samples were more medullated than black hair samples.
- The changes in various hair coat characteristics did not run parallel in all body regions. In summer the coats were uniform over the body. In autumn

and winter, however, various hair coat characteristics varied significantly between body regions.

- All the characteristics considered changed with time. Large seasonal changes were found in percentage of medullated hairs, hair length and melanin content. The seasonal cycle in percentage of medullated hairs – from 50% in winter to 90% in summer –, which represents the seasonal variation in coat composition, was closely related to change in daylength.
- Large changes in coat composition occurred in spring and in autumn. In the heifers used in the shedding experiment in autumn about 50% of the hairs were shed and the increase in hair length resulted from the growth of the 'summer' hairs.
- The melanin content was found to be related to body weight gain.

The hair coat characteristics of Friesian heifers after introduction into Kenya are described in paragraph 3.3. In a preliminary study we made measurements on 25 heifers brought to Kitale in October 1972. The main study was made on 27 heifers brought to Kitale in October 1973. The most important results were:

- The percentage of medullated hairs remained at the same low level (40–50%) during the first 12 months; only after this period it increased gradually. A few months after arrival in Kenya the percentage of fragmentary medullated hairs rose rapidly.
- It was striking that most animals grew very dense coats in the first six months in Kenya.
- Both hair diameter and hair length decreased in the first 6 months in Kenya.
- Only in those periods when the heifers experienced a rather low plane of nutrition did some hair coat characteristics correlate with body weight gain.

Chapter 4 discusses some results from the experimental heifers in the Netherlands and from the heifers examined in Kenya, and presents our conclusions.

The main outcomes were:

- Contrary to the practice, in comparative studies black and white hairs should be studied separately. Moreover the body region chosen for sampling may significantly affect the results.
- The experimental heifers in the Netherlands adapted to the summer conditions by developing a short, medullated, and less dense hair coat. The seasonal rhythm in coat composition is probably due to changes in photoperiod acting through the endocrine system.
- Our results on coat shedding do not agree with those from Australia mentioned in the literature. The sequence of events in temperate zones is probably:

a. in spring most of the hairs are replaced: the non-medullated hairs disappear almost entirely from the coat and almost all the new hairs are medullated;
b. in autumn about 50% of the hairs are replaced: non-medullated hairs appear in the coat again, the hair density increases, and the 'summer' hairs increase markedly in length;
c. some replacement occurs continuously throughout the year.

- In Kenya the equatorial photoperiod probably upsets this cycle in the imported heifers. The low level of medullated hairs during the first 12 months, the marked increase in fragmentary medullated hairs, and the high hair densities in the first 6 months (mainly due to the fact that the non-medullated hairs were shed only very gradually) show that these animals had difficulties in acclimatizing. It took about 18 months before the coat composition of the heifers transferred to Kenya was about the same as that of the heifers in the Netherlands in summer. These results endorse YEATES's (1958) view that the equatorial light environment must be regarded as an extra setback to the successful adaptation of European cattle to hot equatorial regions.
- Contrary to the assumptions in the literature that both hair follicle and hair density decrease as the animal grows and that hair density is not subject to seasonal changes, our findings suggest that a number of follicles producing non-medullated hairs remain empty in the summer months and that the number of empty follicles per unit area is inversely proportional to the number of non-medullated hairs per unit area. This would partly explain the surprizing high hair densities in the first 6 months in Kenya, because in the heifers in Kenya dense hair coats tended to be composed of more non-medullated hairs. We have indications that in animals with extremely high hair densities a number of follicles contain two hairs. So hair follicle population figures are not equivalent to hair population figures.
- Ambient temperature is related to hair length. The influence of temperature may be mediated by the thyroid.
- Plane of nutrition is probably (like in sheep and men) directly related to hair diameter.
- There was no evidence for a strong link between body weight gain and hair coat characteristics. In the Netherlands body weight gain was related to melanin content only; the significance of this relationship is not fully clear. The results in Kenya confirm the assumption of various workers that a medullated coat indicates capacity to react favourably under stressful conditions.
- In the mild climatic conditions of Kitale the hair coat is probably not very important in relation to the thermal balance of the animal. In hot-dry and hot-wet climates heat problems may arise (at least in the first year after exportation) in animals that are transferred from the temperate to equatorial regions. This has to be investigated further.
- Further research is also necessary to reveal the role of various hair coat characteristics on heat transfer. And it will be interesting to investigate the physiological mechanisms underlying the relationships between coat type and thrift in a tropical environment. This should be determined with animals kept under controlled conditions.

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APPENDICES

APPENDIX 1. Data from literature on hair follicle and sweat gland characteristics

Animals	Environment	Hair follicle			Sweat gland				Authors
		length mm	diam. µ	depth mm	length µ	diam. µ	shape	10^{-6} × volume μ^3	
Friesian bulls n = 90	Great Britain	1.9 ± 0.3	52.5 ± 7.5	1.6 ± 0.2	1151 ± 262	139 ± 19	8.3 ± 2.2	18.2 ± 7.2	(1)
Friesian cows n = 52	Great Britain	1.9 ± 0.1	45.9 ± 6.8	1.7 ± 0.1	1034 ± 231	125 ± 15	8.3 ± 1.9	13.2 ± 4.8	
Friesian steers n = 39	Great Britain	1.8 ± 0.2	40.6 ± 6.0	1.6 ± 0.2	913 ± 184	110 ± 10	8.3 ± 1.9	8.8 ± 2.3	
Ayrshire cows n = 18	Australia, NSW^{a}	1.9 ± 0.1	49.8 ± 5.6	1.6 ± 0.1	912 ± 163	122 ± 10	7.5 ± 1.4	10.8 ± 2.7	
Ayrshire cows n = 85	Great Britain	1.9 ± 0.2	42.4 ± 6.8	1.7 ± 0.2	954 ± 289	126 ± 17	7.6 ± 2.2	12.4 ± 5.8	
Shorthorn cows n = 20	Australia, NSW	1.8 ± 0.1	45.7 ± 4.7	1.5 ± 0.1	1023 ± 140	103 ± 10	10.1 ± 1.7	8.5 ± 1.9	
Shorthorn cows n = 45	Great Britain	2.0 ± 0.2	38.2 ± 6.0	1.8 ± 0.2	983 ± 205	109 ± 12	9.0 ± 1.7	9.5 ± 3.9	
Friesian cows n = 17	Australia, NSW	1.7 ± 0.1	44.5 ± 5.7	1.3 ± 0.2	939 ± 191	101 ± 11	9.3 ± 1.6	7.8 ± 2.7	
Friesian cows n = 52	Great Britain	1.9 ± 0.1	45.9 ± 6.8	1.7 ± 0.1	1034 ± 231	126 ± 15	8.3 ± 1.9	13.1 ± 4.8	
Galloway cows n = 28	Australia, NSW	2.4 ± 0.2	42.6 ± 5.5	1.9 ± 0.3	1110 ± 259	111 ± 12	10.0 ± 2.0	11.2 ± 4.3	
Galloway cows n = 30	Great Britain	2.1 ± 0.2	30.6 ± 3.6	1.8 ± 0.2	1061 ± 151	103 ± 12	10.4 ± 1.9	9.0 ± 2.5	
Guernsey cows n = 19	Australia, NSW	1.8 ± 0.2	50.9 ± 4.1	1.5 ± 0.1	894 ± 162	109 ± 10	8.2 ± 1.2	8.6 ± 2.8	
Guernsey cows n = 17	Great Britain	1.9 ± 0.3	45.6 ± 4.5	1.6 ± 0.2	830 ± 181	124 ± 19	6.8 ± 1.6	10.6 ± 5.1	
Jersey cows n = 41	Australia, NSW	1.7 ± 0.1	41.9 ± 6.5	1.3 ± 0.2	742 ± 133	96 ± 9	7.8 ± 1.3	5.4 ± 1.7	
Jersey cows n = 44	Great Britain	1.5 ± 0.1	38.6 ± 4.9	1.4 ± 0.1	745 ± 134	115 ± 11	6.5 ± 1.2	7.9 ± 2.2	
78 European breeds n = 1363	All over Europe	2.0 ± 0.3	44.2 ± 8.1	1.8 ± 0.3	928 ± 276	107 ± 21	8.8 ± 2.5	9.0 ± 5.2	(2)
42 Asian breeds^{c} n = 471	All over Asia	1.5 ± 0.3	47.3 ± 8.0	1.3 ± 0.2	738 ± 87	87 ± 18	8.6 ± 3.1	4.9 ± 3.7	(3)
22 African breeds^{d} n = 281	All over Africa	1.6 ± 0.2	53.5 ± 7.3	1.4 ± 0.2	695 ± 223	85 ± 18	8.4 ± 3.0	4.3 ± 2.5	
9 South American breeds^{e} n = 186	All over South America	1.7 ± 0.2	54.7 ± 8.1	1.5 ± 0.2	972 ± 394	90 ± 15	10.8 ± 3.9	6.7 ± 4.3	
Ayrshire cows n = 112	Great Britain	1.8 − 2.3		1.4 − 1.8	749 − 1044	88 − 135	7.7 − 9.5	5.0 − 14.9	(4)
Friesian cows n = 38	Great Britain	1.7 − 1.9		1.5	822 − 1041	74 − 137	5.8 − 8.3	7.5 − 15.0	
Friesian bulls n = 89	Great Britain		48.8 ± 5.4				8.2 ± 1.9	18.2 ± 7.2	(5)
Friesian cows n = 48	Great Britain			1.4 − 1.6	825 − 1014	126 − 133	6.6 − 7.7	10.4 − 14.3	
Jersey cows n = 32	Great Britain			1.4 ± 0.1	755 ± 115	115 ± 12	6.6 ± 1.0	8.1 ± 2.3	
Ayrshire cows n = 85	Great Britain			1.4 − 1.8	765 − 987	125 − 141	5.9 − 7.0	10.4 − 16.2	(6)
Dairy Shorthorn cows n = 15	Great Britain			1.8 ± 0.1	1103 ± 130	109 ± 8	10.2 ± 1.3	10.3 ± 2.1	
White Fulani cows n = 36	Nigeria			0.9 ± 0.3					(7)
n'Dama cows n = 21	Nigeria			1.0 ± 0.1					
Muturu cows n = 12	Nigeria			0.8 ± 0.2					
Friesian cows n = 9	Nigeria			1.6 ± 0.7					
Ayrshire cows, 21 different body regions n = 5	Great Britain				650 ± 60				(8)
Jersey cows n = 285	Australia, NSW				614 − 770	85 − 111	6.2 − 7.8	3.9 − 7.6	(9)
Sindhi and Sahiwal cows n = 9	Australia, NSW				936	173		22.9	(10)
Jersey, Friesian and Red Poll cows n = 7	Australia, NSW				724	129		10.4	
Sahiwal cows, 25 different body regions n = 4	Australia, NSW				753	121		30.5	(11)
Jersey cows, 21 different body regions n = 4	Australia, NSW				451	78		7.3	

Animals	Environment	Hair follicle			Sweat gland				Authors
		length mm	diam. μ	depth mm	length μ	diam. μ	shape	10^{-6} × volume μ^3	
Jersey heifers n = 2	Australia, NSW							2.7 – 3.9	(12)
Zebu heifers n = 2	Australia, NSW							11.9 – 12.2	
Sindhi and Sahiwal cows n = 9	Australia, NSW summer							16	(13)
	winter							27	
Jersey heifers, 5 different body regions n = 8	Australia, NSW							5.6	(14)
Jersey and Sindhi heifers, 5 different body regions n = 8	Australia, NSW							9.8	
10 breed groups	Australia, Qld[b]							7.4	(15)
Ayrshire cows n = 14	Australia, NSW summer						7.1 ± 0.3	7.8 ± 0.7	(16)
	winter						7.6 ± 0.4	10.7 ± 0.7	
Guernsey cows n = 14	Australia, NSW summer						8.5 ± 0.3	5.0 ± 0.4	
	winter						8.2 ± 0.4	9.0 ± 0.8	
AIS[f] cows n = 14	Australia, NSW summer						10.2 ± 0.5	5.1 ± 0.4	
	winter						9.8 ± 0.3	8.4 ± 0.6	
Friesian cows n = 14	Australia, NSW summer						9.2 ± 0.4	4.8 ± 0.4	
	winter						9.7 ± 0.3	8.3 ± 0.6	
Jersey cows n = 14	Australia, NSW summer						6.5 ± 0.1	5.4 ± 0.3	
	winter						6.9 ± 0.1	7.0 ± 0.7	
Brahman × Shorthorn bulls n = 10	Australia, Qld							8.1 – 11.2	(17)
Rough coated Shorthorn bulls n = 10	Australia, Qld							3.9 – 5.2	
Locally adapted Shorthorn bulls n = 10	Australia, Qld							5.2 – 7.2	
Sleek coated Shorthorn bulls n = 10	Australia, Qld							5.6 – 8.2	
AIS bulls n = 10	Australia, Qld							6.5 – 7.3	

The hair follicle and sweat gland characteristic data given in this table relate to average values and standard deviations for the midside sampling position, except otherwise mentioned.

n: number of animals
a: New South Wales, situated between the latitudes 28° and 39°S
b: Queensland, situated between the latitudes 12° and 28°S; most studies in Queensland have been done north of the Tropic of Capricorn
c: including humped cattle, humples cattle and intermediate zeboid cattle
d: including humped cattle, humpless cattle and European cattle
e: including humped cattle, Criollo's and imported Friesians
f: Australia Illawara Shorthorn
g: progeny of a Shorthorn herd that had bred in tropical Queensland for over 50 years

(1): Jenkinson and Nay, 1968; (2): Jenkinson and Nay, 1972; (3): Jenkinson and Nay, 1973; (4): Jenkinson et al., 1975; (5): Nay and Johnson, 1967; (6): Nay and Jenkinson, 1964; (7): Amakiri and Hill, 1975; (8): Findlay and Yang, 1960; (9): Barker and Nay, 1964; (10): Nay and Hayman, 1956; (11): Pan, 1963; (12): Allen et al., 1963; (13): Hayman and Nay, 1958; (14): Pan et al., 1969; (15): Dowling, 1970; (16): Nay and Hayman, 1963; (17): Dowling and Nay, 1960.

APPENDIX 2. Data from literature on hair follicle and sweat gland density

Animals	Environment	Number per cm²	Authors
Newborn Ayrshire calf	Great Britain	10593 ± 3635	(1)
Ayrshire cows, 21 different body regions n = 5	Great Britain	1871 ± 500	
'Egyptian' bulls, 16 different body regions n = 3	Egypt	2633	(2)
Friesian cows n = 21	Australia, NSW[a]	791 ± 32	(3)
Jersey heifers n = 6	Australia, NSW	1192 ± 56	
Jersey cows n = 12	Australia, NSW	1022 ± 27	
Shorthorn heifers n = 33	Australia, NSW	1041 ± 21	
Shorthorn cows n = 60	Australia, Qld[b], under good conditions	794 ± 20	
Shorthorn cows n = 35	Australia, Qld, under dry conditions	1090 ± 29	
AIS[c] heifers n = 5	Australia, NSW	928 ± 35	
AIS cows n = 29	Australia, NSW	807 ± 28	
AIS cows n = 12	Australia, Qld, under dry conditions	1028 ± 47	
Sindhi and Sahiwal cows n = 9	Australia, NSW	1507 – 1509	(4)
Jersey, Friesian and Red Poll cows n = 7	Australia, NSW	981 – 1005	
Shorthorns at 1 year n = 30	Australia, Qld, under	1324	(5)
at 2 years n = 10	dry conditions	1124	
at 3 years n = 10		1039	
at 4 years n = 15		829	
Shorthorns at 1 year n = 6	Australia, NSW, under	862	
at 2 years n = 6	good conditions	765	
at 3 years n = 8		646	
AIS at 1 year n = 5	Australia, Qld	1206	
at 2 years n = 17		980	
at 3 years n = 6		1040	
at 4 years n = 6		768	
Zebus at 1 year n = 4	Australia, Qld	2022	
at 2 years n = 5		1528	
at 3 years n = 14		1647	
at 4 years n = 8		1565	
Brahman × Shorthorn bulls n = 10	Australia, Qld, winter	1198 ± 128	(6)
	spring	1209 ± 66	
	summer	1261 ± 63	
	autumn	1145 ± 31	
Rough coated Shorthorn bulls, n = 10	Australia, Qld, winter	985 ± 50	
	spring	1004 ± 69	
	summer	1003 ± 71	
	autumn	905 ± 43	
Locally adapted Shorthorn bulls[d] n = 10	Australia, Qld, winter	788 ± 21	
	spring	875 ± 32	
	summer	808 ± 41	
	autumn	749 ± 28	
Sleek coated Shorthorn bulls n = 10	Australia, Qld, winter	1032 ± 46	
	spring	1037 ± 56	
	summer	993 ± 60	
	autumn	864 ± 36	

Animals	Environment	Number per cm²	Authors
AIS bulls n = 10	Australia, Qld, winter	927 ± 46	
	spring	987 ± 51	
	summer	1001 ± 37	
	autumn	883 ± 33	
Jersey heifers, 510 lb n = 2	Australia, NSW	1360 –1620	(7)
Zebu heifers, 420 lb n = 2	Australia, NSW	2080 –2400	
Sahiwal cows, 25 different body regions n = 4	Australia, NSW	1197	(8)
Jersey cows, 21 different body regions n = 4	Australia, NSW	1128	
Ayrshire cows n = 14	Australia, NSW, summer	954 ± 36	(9)
	winter	1040 ± 39	
Guernsey cows n = 14	Australia, Qld, summer	1016 ± 73	
	winter	989 ± 41	
AIS cows n = 14	Australia, Qld, summer	1072 ± 39	
	winter	1064 ± 22	
Friesian cows n = 14	Australia, NSW, summer	1065 ± 48	
	winter	1093 ± 42	
Jersey cows n = 14	Australia, NSW, summer	1004 ± 42	
	winter	959 ± 25	
Hereford, Shorthorn and Hereford × Shorthorn breed groups, follicle number adjusted for body weight (500 lb)	Australia, Qld	874 – 994	(10)
Africander × Hereford and Africander × Shorthorn breed groups, follicle number adjusted for body weight	Australia, Qld	872 – 891	
Brahman × Hereford and Brahman × Shorthorn breed groups, follicle number adjusted for body weight	Australia, Qld	1070 –1110	
Jersey heifers, 5 different body regions n = 8	Australia, NSW	1067	(11)
Jersey × Sindhi heifers, 5 different body regions n = 8	Australia, NSW	1112	
Friesian bulls n = 79	Great Britain	996 ± 169	(12)
10 breed groups	Australia, Qld	825	(13)
White Fulani cows n = 36	Nigeria	1421 ± 672	(14)
N'Dama cows n = 21	Nigeria	1651 ± 864	
Muturu cows n = 12	Nigeria	1665 ± 960	
Friesian cows n = 9	Nigeria	1517 ± 768	

The hair follicle and sweat gland densities given in this table relate to average values and standard deviations for the midside sampling position, except otherwise mentioned.
n: number of animals; a: New South Wales, situated between the latitudes 28° and 39°S
b: Queensland, situated between the latitudes 12° and 28°S; most studies in Queensland have been done north of the Tropic of Capricorn; c: Australia Illawara Shorthorn; d: progeny of a Shorthorn herd that had bred in tropical Queensland for over 50 years

(1): Findlay and Yang, 1950; (2): Hafez et al., 1955; (3): Carter and Dowling, 1954; (4): Nay and Hayman, 1956; (5): Dowling, 1955; (6): Dowling and Nay, 1960; (7): Allen et al., 1963; (8): Pan, 1963; (9): Nay and Hayman, 1963; (10): Turner et al., 1962; (11): Pan et al., 1969; (12): Nay and Johnson, 1967; (13): Dowling, 1970; (14): Amakiri and Hill, 1975.

APPENDIX 3. Data from literature on medullation characteristics

Animals	Environment	Medullation			Authors
		% med. hairs	med. diam.: hair diam.	medulla diam. μ	
Hereford steers n = 30	Australia, NSW[a] summer	87.0			(1)
	winter	23.6			
AIS[c] bulls n = 10	Australia, Qld[b]	97	0.35		(2)
Sleek coated Shorthorn bulls n = 20	Australia, Qld	70	0.26		
Rough coated Shorthorn bulls n = 10	Australia, Qld	4	0.18		
Brahman × Shorthorn bulls n = 10	Australia, Qld, winter	61.3 ± 4.9			(3)
	spring	88.1 ± 2.4			
	summer	100			
	autumn	72.3 ± 5.5			
AIS bulls n = 10	Australia, Qld, winter	24.4 ± 3.1			
	spring	50.2 ± 6.1			
	summer	79.9 ± 5.0			
	autumn	37.3 ± 5.1			
Rough coated Shorthorn bulls n = 10	Australia, Qld, winter	10.3 ± 1.4			
	spring	21.0 ± 5.8			
	summer	29.5 ± 6.0			
	autumn	5.0 ± 0.4			
Locally adapted Shorthorn bulls[d] n = 10	Australia, Qld, winter	27.6 ± 3.1			
	spring	58.8 ± 8.7			
	summer	62.3 ± 6.7			
	autumn	33.7 ± 6.4			
Sleek coated Shorthorn bulls n = 10	Australia, Qld, winter	22.5 ± 3.4			
	spring	38.4 ± 6.0			
	summer	46.4 ± 6.2			
	autumn	19.7 ± 2.8			
Hereford and Shorthorn breed groups	Australia, Qld, autumn	26.2 – 39.3			(4)
Africander × Hereford and Africander × Shorthorn breed groups	Australia, Qld, autumn	60.7 – 64.1			

Animals	Environment	Medullation			Authors
		% med. hairs	med. diam.: hair diam.	medulla diam. µ	
Brahman × Hereford and Brahman × Shortman breed groups	Australia, Qld, autumn	100			
Jersey cows n = 4	Australia, NSW, autumn	88.3		26.7	(5)
Sahiwal cows n = 4	Australia, NSW, autumn	84.7		39.4	
Hereford and Shorthorn breed groups n = 39	Australia, Qld	52.0 – 64.0			(6)
Africander × Hereford and Africander × Shorthorn breed groups n = 30	Australia, Qld	74.0 – 77.0			
Friesian calves at birth n = 90	The Netherlands	99.0 – 100			(7)
MRY^{e} calves at birth n = 56	The Netherlands	100			
Friesian cows n = 18	The Netherlands, winter	64.1			
n = 6	spring	83.3			
n = 2	summer	100			
n = 7	autumn	71.7			
MRY cows n = 8	The Netherlands, winter	65.8			
n = 8	spring	86.0			
n = 7	summer	100			
n = 5	autumn	77.5			
Braunvieh heifers^{f} n = 4	Switzerland	41.4 ± 10.1	0.15 ± 0.05		(8)
Simmentaler heifers^{f} n = 4	Switzerland	38.3 ± 8.6	0.14 ± 0.04		
Holstein heifers^{f} n = 4	Switzerland	26.7 ± 15.9	0.11 ± 0.07		

The medullation characteristic data given in this table relate to average values and standard deviations for the midside sampling position, except otherwise mentioned.

n: number of animals

a: New South Wales, situated between the latitudes 28° and 39°S

b: Queensland, situated between the latitudes 12° and 28°S; most studies in Queensland have been done north of the Tropic of Capricorn

c: Australia Illawara Shorthorn

d: Progeny of a Shorthorn herd that had bred in tropical Queensland for over 50 years

e: Meuse – Rhine – Yssel cattle

f: annual averages shoulder area

(1): DOWLING, 1958; (2): DOWLING, 1956; (3): DOWLING, 1959; (4): SCHLEGER and TURNER, 1960; (5): PAN, 1964; (6): TURNER and SCHLEGER, 1970; (7): KASSAB, 1964; (8): BIANCA et al., 1974.

APPENDIX 4. Data from literature on hair diameter, hair lenth, hair density and hair weight

Animals	Environment	Hair diam. μ	Hair length mm	Number per cm²	Hair weight mg per cm²	Authors
Woolly coated British beef cattle n = 4	South Africa	41.0 ± 17.8				(1)
Sleek coated British beef cattle n = 4	South Africa	43.9 ± 19.7				
Africander cattle n = 4	South Africa	53.7 ± 30.4				
AIS[c] bulls n = 10	Australia, Qld[a]	61.4 ± 6.7			13.7 ± 2.9	(2)
Sleek coated Shorthorn bulls n = 20	Australia, Qld	54.3 ± 5.2			5.3 ± 1.2	
Rough coated Shorthorn bulls n = 10	Australia, Qld	41.2 ± 6.1			21.2 ± 4.8	
Hereford steers n = 30	Australia, NSW[b], summer	38.5	8		16.7	(3)
	winter	43.6	20.4		48.6	
Zebu's	Australia, Qld, summer		4.2	1290	6.8	
	winter		10.1	1234	30.1	
AIS	Australia, Qld, summer		8.1	874	10.2	
	winter		18.0	924	35.8	
10 breed groups	Australia, Qld			825		(4)
Brahman × Shorthorn bulls n = 10	Australia, Qld, winter	56.9 ± 2.4	13.6 ± 0.2		23.1 ± 1.5	(5)
	spring	67.1 ± 2.3	1.2 ± 0.1		10.8 ± 0.8	
	summer	80.3 ± 2.9	6.0 ± 0.1		10.0 ± 0.7	
	autumn	57.3 ± 1.9	10.0 ± 0.2		14.3 ± 1.2	
AIS bulls n = 10	Australia, Qld, winter	53.6 ± 1.5	22.0 ± 0.3		31.0 ± 1.7	
	spring	58.6 ± 1.9	11.2 ± 0.1		12.6 ± 0.9	
	summer	67.4 ± 1.6	12.4 ± 0.3		18.5 ± 1.4	
	autumn	58.7 ± 1.7	15.0 ± 0.7		17.1 ± 1.7	
Rough coated Shorthorn bulls n = 10	Australia, Qld, winter	49.6 ± 1.5	29.0 ± 1.9		36.0 ± 3.2	
	spring	52.0 ± 1.6	17.7 ± 0.3		23.0 ± 1.1	
	summer	59.2 ± 1.9	16.0 ± 0.8		23.1 ± 2.3	
	autumn	52.0 ± 2.5	20.0 ± 0.9		25.1 ± 1.7	
Locally adapted Shorthorn bulls[d] n = 10	Australia, Qld, winter	55.5 ± 1.3	22.2 ± 1.4		25.9 ± 1.7	
	spring	57.1 ± 1.5	11.1 ± 0.3		13.4 ± 1.7	
	summer	60.5 ± 1.3	13.2 ± 0.1		16.7 ± 1.4	
	autumn	52.4 ± 1.3	16.6 ± 1.0		18.7 ± 2.0	
Sleek coated Shorthorn bulls n = 10	Australia, Qld, winter	53.5 ± 1.8	23.0 ± 1.4		37.4 ± 3.0	
	spring	56.9 ± 1.4	12.5 ± 0.3		14.6 ± 0.9	
	summer	62.5 ± 2.1	13.6 ± 0.3		19.7 ± 1.1	
	autumn	52.4 ± 1.5	15.7 ± 1.0		19.2 ± 1.6	
Hereford and Shorthorn breed groups	Australia, Qld, autumn				16.4 – 17.1	(6)
Africander × Hereford and Africander × Shorthorn breed groups	Australia, Qld, autumn				17.9 – 18.9	
Brahman × Hereford and Brahman × Shorthorn breed groups	Australia, Qld, autumn				13.3 – 13.9	

Animals	*Environment*	*Hair diam. μ*	*Hair length* mm	*Number per* cm^2	*Hair weight* mg per cm^2	Authors
Hereford and Shorthorn breed groups	Australia, Qld	42.2 – 47.7				(7)
Africander × Hereford and Africander × Shorthorn breed groups	Australia, Qld	52.9 – 58.5				
Nine herds of AIS cows	Australia, Qld, spring	42 – 47				(8)
Jersey cows, 21 different body regions n = 4	Australia, NSW, autumn	60.9	8.8			(9)
Sahiwal cows, 25 different body regions n = 4	Australia, NSW, autumn	67.9	4.8			
Friesian bulls n = 89	Great Britain	49.9 ± 5.4				(10)
Friesian cows n = 541	Israel	103			9.7	(11)
Hereford cows n = 14	Canada	45.3	29.1	1785	44	(12)
Hereford × Bison and Angus × Bison cows n = 6	Canada	39.2	27.3	5399		
Friesian cows n = 18	The Netherlands, winter	56.4	23.7		24.6	(13)
n = 6	spring	64.5	12.1		6.6	
n = 2	summer	77.8	20.7		27.0	
n = 7	autumn	61.0	23.0		40.0	
MRY[e] cows n = 8	The Netherlands, winter	56.6	34.1		38.4	
n = 8	spring	67.2	23.4		18.2	
n = 7	summer	78.1	22.9		33.4	
n = 5	autumn	61.8	30.4		35.4	
Iskur cows n = 44	Bulgaria, winter	49.2 – 51.1	28.8 – 32.5		10.5 – 10.6	(14)
	summer	70.3 – 78.5	18.9 – 20.1		4.7 – 5.2	
Danish Red cows n = 40	Bulgaria, winter	59.6 – 65.0	19.6 – 24.5		3.8 – 6.9	
n = 39	summer	64.9 – 76.8	13.0 – 15.3		2.6 – 4.2	
Braunvieh heifers[f] n = 4	Switzerland	36.0 ± 4.4	12.1 ± 2.8	1210 ± 342	19.0 ± 6.6	(15)
Simmentaler heifers[f] n = 4	Switzerland	36.1 ± 4.0	13.0 ± 2.7	1126 ± 265	20.4 ± 9.1	
Holstein heifers[f] n = 4	Switzerland	38.0 ± 6.1	10.6 ± 2.9	1435 ± 201	18.2 ± 7.0	

The hair coat characteristic data given in this table relate to average values and standard deviations for the midside sampling position, except in case otherwise mentioned.

n: number of animals

a: Queensland is situated between the latitudes 12° and 28°S, most studies Queensland have been done north of the Tropic of capricorn

b: New South Wales is situated between the latitudes 28° and 39°S

c: Australia Illawara Shorthorn

d: Progeny of a Shorthorn herd that had bred in tropical Queensland for over 50 years

e: Meuse – Rhine – Yssel cattle

f: annual averages shoulder area

(1): BONSMA, 1949; (2): DOWLING, 1956; (3) DOWLING, 1958; (4): DOWLING, 1970; (5) DOWLING, 1959; (6): SCHLEGER and TURNER, 1960; (7): TURNER and SCHLEGER, 1970; (8): SCHLEGER, 1967; (9): PAN, 1964; (10): NAY and JOHNSON, 1967; (11): BERMAN and VOLCANI, 1961; (12): PETERS and SLEN, 1964; (13): KASSAB, 1964; (14): ZDRAVKOV and DRAGNEV, 1970; (15): BIANCA et al., 1974.

APPENDIX 5. Schematic presentation of the animals sampled in the Netherlands, the sampling places, the sampling dates and the hair coat characteristic measurements

Animals	Sampling places	Sampling dates	Hair coat characteristic measurements							
			Perc of med. hairs	Perc. of frag. med. hairs	Diameter of medullated hairs	Diameter of fragmentary med. + non-med. hairs	Hair length	Hair density	Perc. of anagen hair roots	Melanin content
30 Friesian heifers from the 'Minderhoudhoeve'. These heifers were born between February 4th and April 9th 1974	midside	Jan. 1975	x	x	x	x	x	x	x	x
		March	x	x	x	x	x	x	x	x
		May	x	x	x	x	x	x	x	x
		July	x	x	x	x	x	x	x	x
		Sept.	x	x	x	x	x	x	x	x
		Nov.	x	x	x	x	x	x	x	x
		Jan. 1976	x	x	x	x	x	x	x	x
		March	x	x	x	x	x	x	x	x
14 heifers out of the group of 30	midside, black	July 1975	x	x	x	x	x	x	–	–
	midside, white		x	x	x	x	x	x	–	–
6 heifers out of the group of 30	shoulder	Jan. 1975	x	x	x	x	x	x	–	–
	belly		x	x	x	x	x	x	–	–
	midside		x	x	x	x	x	x	–	–
	sacrum		x	x	x	x	x	x	–	–
	shoulder	July 1975	x	x	x	x	x	x	–	–
	belly		x	x	x	x	x	x	–	–
	midside		x	x	x	x	x	x	–	–
	sacrum		x	x	x	x	x	x	–	–
	shoulder	Nov. 1975	x	x	x	x	x	x	–	–
	belly		x	x	x	x	x	x	–	–
	midside		x	x	x	x	x	x	–	–
	sacrum		x	x	x	x	x	x	–	–

Animals	Sampling places	Sampling dates	bleached hairs					black hairs				
			Perc. of med. h.	Perc. of frag. m. h.	Hair length	Hair density	Perc. of anagen h. roots	Perc. of med. h.	Perc. of frag. m. h.	Hair length	Hair density	Perc. of anagen h. roots
6 Friesian heifers from the department of Animal Production at Wageningen. These heifers were born between February 19th and April 20th 1976	midside	Sept. 1976	x	x	x	x	x	x	x	x	x	x
		Oct.	x	x	x	x	x	x	x	x	x	x
		Nov.	x	x	x	x	x	x	x	x	x	x
		Dec.	x	x	x	x	x	x	x	x	x	x
		Jan. 1977	x	x	x	x	x	x	x	x	x	x
		March	x	x	x	x	x	x	x	x	x	x

APPENDIX 6. Monthly means for temperatures, humidity and precipitation for the 'Minderhoudhoeve', during the period January 1975 – March 1976

Month	Temperature (°C)			Rel. Humidity (%)	Precipitation (mm)
	Max.	Min.	Mean		
January 1975	8.3	3.5	6.2	86	53.9
February	6.4	-0.1	2.5	83	23.8
March	7.7	1.6	4.5	83	59.5
April	10.8	3.5	7.2	80	48.4
May	15.0	7.1	11.0	68	32.4
June	19.4	8.9	14.6	68	55.6
July	21.4	12.1	16.9	77	55.8
August	24.7	13.2	18.9	76	45.5
September	19.0	10.1	14.7	83	68.5
October	11.2	4.6	8.7	87	27.1
November	8.0	2.4	5.2	91	79.4
December	5.5	1.3	3.6	89	23.7
January 1976	5.8	1.7	3.9	87	69.5
February	5.5	-0.4	2.5	85	11.4
March	6.6	-1.0	2.7	74	27.2

APPENDIX 7. Schematic presentation of the animals sampled in Kenya, the sampling places, the sampling dates and the hair coat characteristic measurements.

Animals	Sampling place	Sampling dates	Hair coat characteristic measurements							
			Perc. of med. hairs	Perc. of frag. med. hairs	Diameter of medullated hairs	Diameter of fragmentary med. + non-med. hairs	Hair length	Hair density	Perc. of anagen hair roots	Melanin content
30 Friesian heifers brought to Kitale in October 1972. These heifers were born between January 29th and April 23th	midside	Oct. 1972	x	–	x	x	x	x	–	–
		April 1973	x	–	x	x	x	x	–	–
		Oct. 1972	x	–	x	x	x	x	–	–
30 Friesian heifers brought to Kitale in October 1973. These heifers were born between January 27th and April 25th	midside	Oct. 1973	x	x	x	x	x	x	–	x
		Jan. 1974	x	x	x	x	x	x	–	x
		May	x	x	x	x	x	x	x	x
		Aug.	x	x	x	x	x	x	x	x
		Nov.	x	x	x	x	x	x	x	x
		March 1975	x	x	x	x	x	x	x	x
		May	x	x	x	x	x	x	x	x

APPENDIX 8. Monthly means for temperatures, humidity and precipation for the 'A.D.C. Katuke farm', during the period November 1973–May 1975

Month	Temperature (°C)			Rel. humidity (%)		Precipitation (mm)
	Max.	Min.	Mean[a]	Max.	Min.	
November 1973	30.4	11.5	21.0	93.6	30.1	59.0
December	32.6	8.1	20.4	91.5	23.7	5.0
January 1974	33.6	8.4	21.0	89.2	20.8	10.5
February	34.5	9.4	22.0	84.7	20.8	3.5
March	30.5	11.9	21.2	89.9	29.2	87.0
April	30.3	12.3	21.3	93.0	24.9	18.0
May	28.6	12.0	20.3	94.2	35.8	79.5
June	28.6	11.6	20.1	93.6	35.1	147.0
July	26.5	12.4	19.5	92.2	44.9	129.0
August	27.2	11.9	19.6	94.1	44.3	73.0
September	29.2	11.0	20.1	93.6	36.5	63.0
October	30.7	11.2	20.0	93.2	30.0	86.5
November	29.5	10.6	20.1	91.9	28.5	14.0
December	30.9	9.2	20.1	87.0	21.3	8.0
January 1975	33.1	10.1	21.6	85.0	20.5	9.0
February	33.5	11.3	22.4	82.8	20.1	6.0
March	33.0	12.8	22.9	88.0	21.9	37.0
April	29.7	13.0	21.4	88.0	28.8	87.5
May	29.8	12.9	21.4	93.2	33.5	155.5

a: The mean temperature is taken to be equal to the average of the maximum and the minimum for that month. This is not always correct but according to Griffiths (1976) the approximation is usually good to within about 0.6°C.

SAMENVATTING

Dankzij een overeenkomst tussen Kenyaanse en Nederlandse regeringsautoriteiten, betreffende de export van enkele duizenden zwartbonte pinken naar Kenya, ontstond de gelegenheid om mogelijke adaptatieproblemen van deze dieren te bestuderen. Binnen het kader van de NUFFIC (Netherlands Universities Foundation for International Co-operation) werd een onderzoekproject opgezet getiteld: 'Adaptation of Dutch Friesian heifers in the Tropics, with special reference to Kenya'. Dit project had betrekking op verschillende aspecten, zoals gezondheidskenmerken, vruchtbaarheid en groei. Dit proefschrift behandelt de veranderingen in het haarkleed bij de naar Kenya overgebrachte pinken.

Haarkleed kenmerken en de cyclische veranderingen in deze kenmerken zijn een belangrijk aspect van de ecologische aanpassing van runderen. Het haarkleed vormt de overgang tussen het dier en zijn omgeving en is een weerspiegeling van de reactie van het dier op die omgeving. Voornamelijk Australische onderzoekers hebben gewezen op het belang van het haarkleed als een indicator van het vermogen van vleesrunderen om zich aan te passen aan een warm klimaat. Op dit gebied bestaat geen informatie betreffende melkrunderen.

Ter aanvulling van ons onderzoek in Kenya bestudeerden wij ook veranderingen in het haarkleed van zwartbonte pinken in Nederland; dit omdat er zeer weinig bekend is over het haarkleed van runderen in Europa.

Het literatuurhoofdstuk (2) geeft een overzicht van haarfollikel, zweetklier en haarkleed kenmerken, en hoe deze verband houden met warmte-uitwisseling, produktie kenmerken en adaptatie.

Hoofdstuk 3 geeft de resultaten van ons onderzoek weer. De volgende haarkleed kenmerken werden bepaald: percentage mergharen, percentage fragmentarische mergharen, haardiameter, haarlengte, haardichtheid en percentage haarwortels in de actieve fase van de haargroeicyclus. Alle kenmerken ondergingen bij de pinken in Nederland significante veranderingen in de loop van het jaar.

Grote verschillen traden op in het percentage mergharen (het percentage mergharen volgde een sinusvormig verloop met een maximum van ongeveer 90% in de zomer en een corresponderend minimum van ongeveer 50% in de winter), de haarlengte (de haarlengte bereikte zijn maximum aan het eind van de herfst, de haren waren dan ongeveer 2 maal zo lang als in lente en zomer) en het melanine-gehalte (het melanine-gehalte volgde een parabolisch verloop met het minimum in de zomer). De seizoens veranderingen in het haarkleed zijn een duidelijk voorbeeld van het fysiologisch aanpassingsvermogen van een dier. De 'wintervacht' heeft een veel groter isolerend vermogen dan de 'zomervacht', terwijl de kenmerken van de 'zomervacht' verband houden met een meer efficiënte verdamping via de huid. Het seizoens ritme in het percentage mergharen, dat de seizoens variatie in haarkleed samenstelling in belangrijke mate

weergeeft, wordt gereguleerd, waarschijnlijk via het endocriene systeem, door de variatie in de daglengte.

Er bestaan in de literatuur twee volledig tegenovergestelde opvattingen ten aanzien van het verharen. Eén opvatting is dat een follikel 2 haren per jaar vormt en dat zowel in de lente als in de herfst een bijna volledige verharing optreedt. De andere opvatting is dat de verharing alleen in de lente plaats vindt en dat in de herfst de haren alleen sterk in lengte toenemen. Beide gaan ervan uit dat er geen seizoens variatie in haardichtheid is. Onze resultaten leidden tot de volgende veronderstellingen:

a) in de lente wordt een groot deel van het haarkleed vernieuwd: de wolharen verdwijnen bijna geheel uit de vacht en bijna alle nieuwe haren zijn mergharen.

b) in de herfst wordt ongeveer de helft van het haarkleed vervangen; wolharen worden weer gevormd waardoor de haardichtheid toeneemt en de 'zomerharen' worden aanmerkelijk langer.

c) enige verharing vindt gedurende het gehele jaar plaats.

In Kenya verstoorde de equatoriale daglengte waarschijnlijk het ritme in haarkleedsamenstelling bij de geïmporteerde pinken. Zo bleef het percentage mergharen gedurende de eerste 12 maanden in Kenya op ongeveer het niveau van de wintervacht van de pinken in Nederland. Pas na 18 maanden bestond er een overeenkomst in haarkleed samenstelling tussen de pinken in Kenya en die in Nederland in de zomermaanden. Het was opvallend dat veel dieren in de eerste 6 maanden van hun verblijf in Kenya een grote haardichtheid per eenheid huidoppervlakte vertoonden. Bovendien traden er grote individuele verschillen op wat betreft dit kenmerk. Deze grote haardichtheden werden veroorzaakt doordat 1) de wolharen slechts zeer geleidelijk uit de vacht verdwenen, 2) er een sterke en onverwachte stijging optrad in het aantal fragmentarische mergharen.

In Kenya verminderde de haarlengte van de geïmporteerde pinken, reeds na enkele maanden, met ongeveer 50%. De temperatuur beïnvloedt waarschijnlijk via de schildklier de haarlengte.

Onze bevindingen toonden aan dat de pinken in Kenya problemen hadden met de acclimatisatie aan hun nieuwe fysische omstandigheden. Echter, onder de klimaatsomstandigheden in het gebied in Kenya waar deze pinken verbleven zal het vachttype, dat deze pinken in de eerste 6–12 maanden van hun verblijf in Kenya vertoonden, geen belemmering vormen voor de warmte-afgifte. De geïmporteerde pinken verbleven in Kenya namelijk in een gebied gelegen op een hoogte van ± 1900 m en de gemiddelde temperatuur per maand tijdens ons onderzoek varieerde slechts tussen 19.5°C en 22.9°C. Korte, dikke merghoudende haren zijn vooral van belang in een warm en vochtig klimaat.

Er was geen overtuigend bewijs van een verband tussen gewichttoenames en haarkleed kenmerken. In Kenya bestond er slechts in die maanden, waarin het voedingsniveau vrij laag was, een relatie tussen gewichttoenames en haarkleedkenmerken. Dit onderschrijft de conclusies van diverse Australische onderzoekers dat een glanzend merghoudend haarkleed een aanwijzing is van adaptatie aan moeilijke omstandigheden. Nader onderzoek is noodzakelijk naar de fysiologische achtergronden van deze relaties.