

Researching Colour Patterns In The Lynton Feral Goat

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1. A system for identifying feral goats in the field

Although I have now been studying all aspects of goats for nearly 50 years, it is only in the last 20 years that I have begun to make proper sense of the genetics of their colour patterns.

My close interest in coat patterning in goats began with the Lynton herd of feral goats. To properly manage them I needed to be able to identify individuals very quickly. Over time I was able to distinguish goats by their overall look, the way in which they moved, and their character and temperament. But in the early days I needed a check-list identifier based on combinations of colour characteristics. And so it was that I began to record every detail of every goat in relation to their appearance.

The only literature available to me at that time related mainly to the inheritance of coat colour, being based upon herd book descriptions of colour in registrations (Asdell and Buchanan Smith, 1927) and hair samples taken from the sides of goats (Hards, 1950). The interest here was in the range of colours exhibited in the goat, and whether they were dominant or recessive in relation to each other. No research had been carried out on colour patterns during this period, although Hards did suggest that “Swiss” markings were linked, and thus inherited as a ‘bundle, whilst Asdell and Buchanan Smith stated that a black dorsal stripe was linked to black points. Hards, on the other hand, was of the opinion that the dark dorsal stripe was inherited separately, these three conclusions being the published extent of any knowledge relating to the genetic linking of markings. Armed with the foregoing, I set about my own research into the inheritance of coat characteristics in goats.

The Lynton feral goat herd descends mainly from 3 Cheviot goats- originating in the College Valley, Northumberland- which was introduced into the Valley of the Rocks in December, 1976. At the time I recorded their colours in the following way: The male was grey with a tan sheen and black legs; the older female a “drab” colour that I later called blackish-grey, also with black legs; and the younger female black with a reddish sheen and striped legs. These interbred with 3 males of Saanen type and colouring, one of which was polled. At least one of these males had a very light sandy roaning to the coat. The significance of this escaped me at the time, although I later read Swiss research that suggested this was indicative of such goats being heterozygous for their white colouring. Later, a Bagot female was introduced into the herd. She was ‘well marked’ with black forequarters and white hindquarters, and had a small white stripe above the eye. From these mixed beginnings, the type of the Lynton feral goat was later to emerge.

Initially, I concentrated on the basic colours of the goats, dividing them into 3 basic types: white, which I called ‘Saanen white’, grey and black. As time went on, it became apparent that this schema was over-simplified. With the arrival of the Bagot goat, which was actually black, it became clear that ‘black’ in the Cheviot stock meant of a reddish or rusty hue, even

mahogany, whilst some goats looked to be almost chocolate. I therefore termed the goats I had previously thought of as black 'dark', simply meaning not grey in the grey range. In the 'grey' goats there was the possibility of a light and pure grey, a grey with a tan sheen, or a very dark and smokey grey that I first thought of as drab. Thus, basic colour and shade became the starting point for a recognition chart.

There also appeared to be degrees of roaning. The drab colour I had identified appeared to be a dark roan, hence 'blackish grey', although there were also goats with a basically dark coat and varying smatterings of white hairs, rather like an incomplete roaning.

According to Asdell and Buchanan Smith, roaning was the intermixing of white hairs with any basal colour. They defined blue or grey as being a black, chocolate or fawn roan, and roan as being a brown, red or tan roan. On this basis, the grey goats in the Lynton herd were a black roan and the greys with tan roaning a red or tan roan. At this point (1977) Joan Shields published her book on Exhibition and practical Goatkeeping, and in this she described the cheviot goat as being either a blue or a fawn roan. Blue related to a pure grey, but fawn roan was surprising as I understood fawn to mean a 'yellowish brown', the other roans in the herd looking distinctly tan or red rather than a dull yellowish tan. Interestingly, Hards pointed out that roaning might be minimal, meaning that a goat that appeared to be black might actually be a grey. This, I felt, might explain the minimal roaning in some of the dark Lynton goats.

Hards also stated that there were 2 kinds of black- a very intense jet black and a rusty black. She suggested that we needed to look for black modifiers in the jet blacks, which would modify the intensity of the black. Could this, I wondered, explain the reddish-black coat of the dark Lynton goats?

Goats were born that had a clear pattern of tan (fawn) hairs on a dark coat. Thus the back, sides and legs were dark, but the muzzle, cheeks, the top of the ears, neck, brisket to knee, tail, rump, flank and rear leg to the hock, were fawn. These mostly developed into dark goats with a reddish sheen. Although some adults had distinct fawn patches on the neck, between the ears and less often on other parts of the body. These kids and adults were called 'fawn patterning', and I wondered why most to all of the distinct fawn areas disappeared with maturity.

Having identified the basis colours, I went on to set up a theoretical model that would cover all the basic colour type combinations in the Lynton herd. There would be 9 in all:

1. White
2. Uniform black
3. Black with light roaning (scattered white hairs in coat)
4. Reddish black
5. Reddish black with light roaning
6. Pure grey
7. Mahogany-grey (grey with tan roaning)
8. Blackish grey (a very dark roan, first called 'drab')
9. Mahogany blackish grey (blackish grey with tan roaning)

All were identified in the herd at one time or another, although 1 was eradicated during the mid-1980's, and 2 and 3 did not persist.

I then began to look at secondary characteristics. These, in the main, affected the distal parts. Some goats had black legs, others striped. The belly was black, grey or white; the perineum black or white. Some goats had a white chin patch; some little white eye diamonds above the eyes, and there was often a white lower lip. More rarely, a goat might have a complete face stripe. The muzzle was dark or grey, rarely white; the inside of the ear dark or white; the outside of the ear dark, grey or tan. Some goats had a tan patch on the cheeks, grey or tan roaning, sometimes speckling; and some had the whole of the ear and its surround grey to whitish.

The head was variable, too, with 6 types being identified that ranged between uniformly black and uniformly grey. These were:

1. All black
2. Black with a grey muzzle
3. Black with a grey muzzle and cheeks
4. Grey with a black forehead and face
5. Grey with a black forehead
6. All grey

Pied goats occurred. All of the original 3 College Valley goats were pied, the white patching being confined to the flanks. For the first few years the white patching continued to be confined mainly to the mid-region of the coat: what I thought of as an incomplete belt as there was a dark saddle. Later, random white patching occurred, and over the years the herd became progressively whiter in its markings. This was accelerated by the introduction of the Bagot female, although it wasn't the whole story by any means.

I was now set to go, finding that I could easily and quickly identify goats by their head patterning in conjunction with their combination of coat and leg colour. This was identification to a formula, which helped tremendously when trying to record the intricate social interactions of anything up to 50 plus goats at any one time.

But my field research wasn't the whole story. After several years of collecting data on the goats, I began to wonder whether I was seeing a pattern in the way in which the various colour characteristics occurred. I was encouraged to pursue this when I recalled that Hards had mentioned that the Swiss characteristics were inherited 'as a bundle'. Could this be more widely true of my secondary characteristics? I had a body of data by then, so contrived a card system that enabled me to match up hundreds of characteristics and test my hypothesis.

We will look at my initial results in part 2.

2. Discovering colour patterns and what lies behind Piebaldng

Having collected a body of data on the colour and secondary characteristics of the Lynton feral Goat, I was in a position to test out the hypotheses that some of these at least were linked in the same way that the colour pattern of Swiss goats is inherited as a bundle, which is to say, for example, that a goat with white insides to its ears and a black coat will also, as in always, have a white belly.

After researching endless combinations, I came to the following conclusions:

- White eye diamonds, insides to the ears, a white lip, throat patch, belly and perineum were generally found on the same goat. These characteristics were associated with either a grey or a dark coat when the legs were striped, but not with a grey coat when the legs were black. I called the dark goats with striped legs ‘dark striped legs’, which was pretty obvious, really; and the grey goats with striped legs ‘grey striped legs’. Both types therefore had 6 other characteristics that were quite stable in combination, and I believed that I had discovered 2 stable colour patterns.
- Grey goats always had black or striped legs, but never grey.
- Tan cheeks and outer ears could be found on a goat irrespective of coat or leg colour. Likewise, a grey muzzle and grey on or around the ears could be found on a goat irrespective of coat or leg colour. Thus, these seemed to be general characteristics that were not linked to any particular pelage or leg colour.

The next revelation concerned what is now generally termed ‘co-dominance’. In my early days of working with the Lynton feral goat herd I knew nothing of this, but I discovered its principle with only a hazy understanding of its significance. What I did realise, even so, was that the colour patterns I had discovered could combine in the phenotype to give a completely different pattern to its components.

When I had put various colours and characteristics together to form patterns, I realised something very interesting. The original three College Valley goats had been either dark with striped legs or grey (either grey with a tan sheen or blackish grey) with dark legs. But early on in the herd’s history kids were born that were grey with striped legs. Not only that, but they also had the 6 secondary characteristics that were associated with a dark coat and striped legs. In other words, they were exactly like the dark striped-legs goats excepting that their coat was grey. I fathomed that these goats had to be a cross between the greys with black legs and darks with striped legs: grey being dominant in the coat and white overlaying dark anywhere that it appeared on the body or distal parts. I had therefore discovered co-dominance in the inheritance of coat characteristics in goats, but failed to realize its full input for many years to come.

White patching, according to the available literature, was inherited separately and dominant. My study, however, suggested that it was a recessive, and I felt quite out of step with the then accepted research.

As I watched the herd develop, and the incidence of white with it, I began to speculate on how white patching might be inherited. Intriguingly, in goats that were predominantly white,

the dark areas appeared as quite symmetrical spots and patches, looking like they were superimposed on a white base rather than the other way around, which was a forewarning that any study of the inheritance of white mismarking was going to be complex in the extreme.

Apart from an allele for white patching, which Asdell and Buchanan Smith called ‘an extension of white spotting’, and Hards ‘piebald’ or ‘white mismarking’, there had to be some mechanism that controlled where it occurred, but its mechanics defeated me. Hards suggested that piebald was a series with a cline between a black goat with a few white hairs and a white with black skin spots, a mating of these two extremes producing a piebald kid that was somewhere in the middle. This suggested that the amount of white spotting varied greatly in the genotype of goats, and that the phenotypic white coat pattern in any animal was the amalgamation of two genotypes, and thus unique to that animal. Thus, endless combinations would be occurring. My difficulty with this was that my study of the Lynton herd suggested that there were clear patterns of piebald markings as well as more random spotting. To confirm this I studied hundreds of photographs of pied goats, field researched every feral herd in Wales, and visited over a dozen domestic herds in which the goats were predominantly pied. Finally, I came up with a working hypothesis: what if there were not only alleles that controlled spotting at mini-locations, giving what appeared to be random white spots, patches and larger areas, but alleles that controlled white spotting over distinct parts of the body in blocks, which would give easily recognizable piebald patterns? To test this, I divided the body into distinctive key areas. These I designated to be the belly, sides, upper back, legs, rump, neck and head. I further speculated that each of these not only acted independently in terms of inheritance, but could be combined in certain ways to make even more distinct patterns. Thus, my theory was that the Schwarzhals breed had a distinct and heritable pattern that demarked black forequarters and white hindquarters at the mid-line of the body, whilst the Bagot goat was either a breed with a similar heritable pattern but with additional alleles for random spotting, or simply a breed with random white spotting that had been largely but unsuccessfully selected for dark forequarters and light hindquarters. I had therefore come to the conclusion that the inheritance of white spotting in goats was far more complicated than I had first thought, and most certainly more complex than the available literature would suggest. Not only was there random white spotting in which the body was sub-divided into mini-locations with the potential to be pied or not, but distinct pied patterns as well.

I tested this idea out on Bagot goats; further speculating that white would appear on the phenotype anywhere that it appeared on either genotype of the sire and dam. The idea seemed to hold up. I was a put off, however, when one Bagot goat breeder of renown reviewed my findings and faulted them on the basis that the herds I had used for analysis were grades-‘rubbish’, as he put it- and not purebred stock. This greatly discouraged me, then encouraged me to test the hypothesis that each goat inherited two distinct patterns, but showed only one in the phenotype, it being a combination of the dominant two patterns, one from the sire and one from the dam, that showed as a different co-dominant pattern in the offspring. I wrote this up as:

‘A goat inherits a distinct white pattern from each of its parents. Because each pattern is co-dominant, white will show anywhere in the phenotype of the kid where it shows on either parent’s passed on genotype. This means that the patterning of the phenotype will always be different from the patterning of either parent. As, in a similar way, the

sire and dam show a co-dominant pattern, we will never be able to see either of the genotypic patterns that a goat inherits. This seeks to explain why it is so difficult to maintain the well-defined 'Bagot markings' that were said to typify the breed, as there are no clues to the inherited pattern in the phenotypic pattern.'

I couldn't really make this work or find a way to prove this, however, and returned to my 'rubbished' hypothesis. In doing so, I felt that I had adequately explained that the white side patch in the College Valley goats might be inherited separately in much the same way as Galloway cattle inherit their belt. This being the case, it was likely therefore, that the typical pattern of the College Valley goats was an 'incomplete belt'. I called this hypothetical block white pattern 'belted' after the Belted Galloway breed.

Another aspect of white patching that I found to be intriguing was the commonality of a white patch on the forehead. At first I assumed that this was due to inbreeding, as in the herd lacked the allele for white spotting on the mini-location of the forehead, but later came to the conclusion that it might be inherited separately like the 'belt'.

At this point I had many ideas about colour inheritance in goats that were based upon the Lynton herd, but no clear ideas about how the whole jigsaw fitted together. Then I came across the genetics of colour inheritance in sheep. I had already reached the conclusion that goats and sheep were closely related, but the work of Sponenberg (summarized in 1997) in relation to colour inheritance in sheep gave me the opportunity to make direct comparisons with goats generally. Many aspects of my work now became clearer. We will look more closely at this in part three.

3. Separating the sheep from the goats

As I read through the research into the genetics of colour in sheep, which was published between 1976 and 1986, I was struck by the fact that it centred upon distinct colour patterns at the Agouti locus. In essence all goats were black with tan patterning that could affect the body and distal parts. Overall, there was a cline between all black (no patterning) and all tan/white (all patterning).

I had already concluded that there were links between many of the characteristics I had recorded in the Lynton herd, but this was an opportunity to test whether these were valid patterns in that there were parallels with sheep. To my astonishment, the linked characteristics that I had termed 'dark striped legs' had an almost exact parallel in the sheep allele called light belly or black and tan (At) The coat is black, but the belly, perineum, throat, insides to the ears and stripes above the eyes are tan, usually diluting to white. This was my dark stripe legs, although there was no mention of a white lower lip in sheep. This helped establish that the light belly pattern is found in the Bagot goat, as the Bagot female introduced into the Lynton herd had white eye diamonds. Encouraged by this, old photographs of the Bagot herd in Bagot park during the early part of the last century were studied, with further confirmation of the light belly pattern in the breed prior to its grading up.

A second allele was grey and tan (Agt), described as appearing to be phenotypically as the grey pattern combined with the black and tan pattern. The grey and tan pattern was manifestly my grey striped legs, although in the Lynton herd this colour pattern was a co-dominant

outcome of crossing a grey with black legs and a dark with leg stripes. It was interesting in this respect that we had two identical colour patterns, one being inherited as an allele in sheep, the other being a combination of two separate alleles in goats.

This led on to a search for the grey pelage with black legs and varying degrees of black on the head- with or without tan hairs intermingled- that was a feature of Lynton goats. There were a number of candidates for this pattern. Firstly there was grey (Ag), which was described as having a white undercoat and a black outer coat. A variant was Gotland grey (Agg) which was a darker grey. There seemed to be some doubt as to whether Gotland grey was an allele in its own right or a dark variant of grey brought about by selection. This was important as I was familiar with the Gotland breed, and aware that it had black legs and head. There was also a light grey (Akg), which was lighter than the standard grey pattern. Lastly, there were the blue (Abl) and light blue (Albl) colour patterns that replicated the badgerface or dark belly allele, but in grey rather than tan. In the blue alleles the coat was grey but the belly, perineum, lower leg, inside of the leg, eel stripe, shoulder stripe, stripe up the underside of the neck, lower jaw, the inside of the ears and parts of the head in a pattern were black. Certainly the Lynton greys with black legs had black insides to the ears, but little else fitted. Lastly, there was roan (RN) at a separate locus. In sheep this was a type of white spotting, and known as dominant lethal roan as the homozygous kids died early. Heterozygotes were viable and tended to have an even mixture of white and coloured hairs. It was pointed out that roan on black produced a grey, and that it was important not to confuse this with the grey caused by the Agouti series (Ag), meaning that they must be very similar. So there we had it, and it required some detective work to try and sort out which of the grey colour patterns in sheep, along with grey roan, was the most likely equivalent to the Lynton grey with black legs in the Lynton goat. The blues were eliminated straight away, as the Lynton greys did not have the distinct patterning of the black belly alleles. Grey was promising, as the link between grey and Gotland grey suggested that this allele had a black face and legs. But it could easily be confused with grey roan, which also had black legs and head. One factor militating against the Lynton greys being grey roan was the query as to whether homozygous grey roan was as lethal in goats as it was in sheep? A second was that until the early 1950's, the Cheviot goat was only grey in colour, meaning that there were no blacks as would have been expected had the grey been roaning. It seemed, on balance therefore, that the Lynton greys with black legs were grey patterning (Ag) in the Agouti series.

Sheep colour genetics didn't really help with the quest to make sense of tan hairs in grey coats, although there were some possible clues with regard to reddish black. The colour pattern called sooty was described as being a uniform mixture of black and tan hairs, which sounded very much like a roan colour pattern at the Agouti locus. Then there was light red cheek (Apc) which sounded very much like sooty but with red cheeks. Lastly, there was eyepatch (Aep), which had tan areas around the eyes and a tan and black coat. If sheep could be either a uniform mixture of tan and black, and additionally have tan patches on the cheeks or round the eyes, then it was perfectly possible that the reddish black Lynton goats were a colour pattern in their own right and not black with modifiers, whilst the goats with tan cheeks, and possibly tops to their ears, were also a colour pattern. Goats corresponding to 'sooty' in sheep I called reddish black still, whilst those with tan on their cheeks as well I called 'tan cheeks'. I had, at first, pondered whether the reddish black goats were chocolate, meaning a dark brown. But the research into sheep had shown that the Brown locus is responsible for replacing any areas on the goat that are black with brown. As those Lynton goats that showed

what may have been a chocolate coat retained a black head and legs, it was reasoned that they were tan rather than dark brown. The linking of reddish black with tan roaning at the Agouti locus therefore held up, and it seemed likely as well that the reddish blacks and tan cheeks were one and the same.

The colour genetics of sheep dealt with the spotting locus at some length. It was a recessive, which came as a relief. It suggested overlapping phenotypes, rough symmetry on each side of the body and the commonality of spotting on the distal parts of heads and limbs. Its extent was said to be variable, suggesting either different spotting locus alleles or modifications at other loci. Yes, it was complex; yes, it could produce a nearly white animal by selection: but it didn't answer my question as to whether or not there was a separate mechanism or mechanisms of inheritance that produced either large, well-defined patterns or small localised ones alongside randomly presented spotting.

Then, joy of joys, I discovered the E locus allele and the Pigmented Head allele. The E locus allele produces the well known pattern in sheep that is associated with the down breeds: a white body and neck, and black head and legs. I was already familiar with the Somali Black headed sheep in wildlife parks, and had speculated as to whether this was a colour pattern. As it turned out it was, being found at the Pigmented head locus. In this breed either the head only or the head, neck and a part of the shoulder is black, the rest of the body white. This allele is called the 'Persian', after another breed with this pattern. The Dorper breed, which has now been imported into Britain, also has the Persian allele and therefore shows this pattern. Other alleles at the pigmented head locus are the Turkish and the Afghan lethal, which produces white goats in which only some areas around the head and legs- eyes, ears, knees and hocks in the Afghan lethal, and noses, eyes, ears and distal legs in the Turkish-remain pigmented. Further encouraged by this, I made a search of goat breeds world-wide, adding the Wuan breed of China and the Boar goat of South Africa to possible equivalents of the Persian allele in sheep. What was important, however, was that I felt that I now had sufficient evidence to suggest that the white side panel in the Cheviot goat and possibly also the well-known patterning of the Bagot goat were due to alleles at a separate locus to that which produced random spotting.

By the time that I had read through the literature pertaining to colour genetics' in sheep, I had confirmed that there were, in fact, linkages between markings or characteristics, and that these consisted of heritable patterns; confirmed that these colour patterns were co-dominant; confirmed that the inheritance of white spotting was recessive, and not dominant as previously thought; and further confirmed that aside of random spotting, there were alleles for distinctive patterns that affected certain parts of the body. I had also found a colour pattern in sheep that could be paralleled in the Lynton goat by the crossing of 2 colour patterns.

I was also able to link the reddish black coat of the Lynton goat with colour patterns in sheep that were associated with a mixture of black and tan hairs (dark reddish to mahogany in the Lynton goats), and the tan cheeks of many Lynton goats with this phenomenon.

Being made aware of the likelihood that the reddish-tan goats in the Lynton herd were a mahogany-black roan focussed my attention on coat colour again, and in particular the roaned coats numbered 6 to 9 in my original assessment. These were:

6. Pure grey
7. Mahogany grey (grey with tan roaning)
8. Blackish-grey
9. Mahogany blackish grey

A theoretical model of co-dominance in the inheritance of roan coat colour was then devised in which the following was assumed to be true: 6 would be white-grey in equal measure; 7 a mixture of white, tan and black; 8 a mixture of black and white in which black dominated, and 9 was a mixture of mahogany, black and white in which black dominated the two tan colours.

The base colours, judging from the known pattern of inheritance, were considered to be:

1. Uniform black
2. Mahogany-black
3. Grey, meaning pure grey or a mixture of black and white hairs

Given the foregoing, the outcomes would be that a combination of 1 and 2 would result in a coat that was three-quarters black and a quarter red; 1 and 3 would result in a coat that was three-quarters white and a quarter grey; and 2 and 3 would result in a coat that was half black, a quarter white and a quarter tan.

Comparing the theory with the colour types, a combination of 1 and 2 is close to colour type 9; a combination of 1 and 3 is close to colour type 8, and a combination of 2 and 3 close to colour type 7.

By looking at all 9 colour types, I was able to discern variability in the intensity of roaning in relation to grey, which is to say the introduction of white hairs into a black coat. What I was trying to do here was to account for the tan roaning that seemed to be present in either an otherwise grey coat or a distinctly blackish grey coat. To date, the logic of the known data would suggest that roaning only introduced white hairs into the coat, whereas my experience of the Lynton herd in relation to known colour inheritance in sheep would suggest that roaning could involve undiluted tan hairs as well, albeit in a specific colour pattern rather than roan at the roan locus. If this were so, then the introduction of a standard roan (white hairs) into a mahogany black roan should produce a coat with a mixture of white, tan and black hairs. Given this, my theory held up. Well, almost. This appeared to be further evidence that grey goats in the Lynton herd were roan rather than a distinct colour pattern.

What I couldn't do at this time, was make sense of grey muzzles and ear tops; white forehead patches and tan ear tops, in relation to sheep. Nor was I any closer to making sense of the strange-coloured and symmetrical spots that had turned up in the early Lynton goat.

This will be considered in part 5.

4. Grizzled grey muzzle, a new and independently inherited pattern in goats

Twenty-seven of the goats in the Lynton herd had black heads with various combinations of tan roaning (ranging from white, through cream and reddish-tan to dark mahogany) on the muzzle, cheeks and upper ears. This was irrespective of whether the basic colour pattern was mahogany or lightbelly. Numbers and overall percentages were as follows:

- 21 (78% or a little over three-quarters) had a grey muzzle
- 11 (41%) had grey cheeks
- 13 (48%) had tan or cream cheeks
- 12 (45%) had grey ears
- 16 (54%) had tan or cream upper ears
- 4 (15%) had an intermingling of grey and tan on the cheeks
- 6 (22%) had an intermingling of tan and grey on the upper ears

- 15 (55%) had all roaning on the muzzle, cheeks and upper ears
- 12 (45%) had a combination of a grey muzzle and grey upper ears
- 15 (55.5%) had a combination of a grey muzzle and grey or white ears

Of the goats with grey muzzles, 6 (22%) had either a dark cheek or dark upper ear. Of the goats with dark muzzles, 3 (11%) had either a dark cheek or a dark muzzle.

Grey muzzles were typical, white, whitish or pale tan muzzles being very rare. Either grey or tan/cream cheeks were found in roughly equal measure, as was either grey or tan/cream upper ears. Roaning of any colour or shade usually affected the top of the upper ear, surrounded by a dark rim, being less intense to not discernible towards the base. More rarely, the whole ear was roaned, including the base, more rarely still, the whole ear was white to whitish.

The cheeks were roaned with varying intensity, ranging from the appearance of uniform tan to a hardly discernible speckling.

I began with what I felt I knew, this being the colour patterns pale red cheeks and eye patch found in sheep. In these patterns the cheeks and areas around the eye are tan. Seven of the sample goats clearly showed this pattern (26%). Of these, two had dark muzzles and 5 grey. Also, there seemed to be a clear link between tan cheeks and upper ears that did not hold for grey muzzles. I therefore postulate a colour pattern that I called 'tan cheeks'. This pointed to co-dominance, but what?

15 goats (55%) also showed a clear combination of grey muzzles and upper ears. This seemed to be significant when reviewing all 27 goats, and a distinct pattern was postulated that I termed 'grizzled grey muzzle'. If this were so, then this otherwise unidentified pattern would be co-dominant with tan cheeks. Three of the goats clearly showed this pattern, which was encouraging.

I then investigated the variants.

The first set of variants investigated was clustered around my grizzled grey muzzle. 75% of the goats in this category showed a variant pattern, which is to say that they did not have both a grey muzzle and grey ears.

Goats that were not a co-dominant pattern, but pure grizzled grey muzzle, fell into 3 variants. These were a grey muzzle with:

- Tan upper ears
- Tan and white upper ears
- Dark upper ears

It was thought that a grey muzzle with tan upper ears was either a genuine pattern in its own right, or a grizzled grey muzzle in which the otherwise white roaning on the upper ear had not diluted from tan (suggesting modifiers to control the colour/shade of tan). Tan and white upper ears may have been, in actuality, a combination of mahogany and grizzled grey muzzle in which the apparently black cheeks were really a very dark mahogany. To support this possibility, my field notes did record goats with apparently uniformly black heads that on closer inspection were found to have very dark mahogany cheeks. A grey muzzle with dark upper ears may have been a grizzled grey muzzle in which the grey speckling was almost non-existent. This would suggest a roaning cline in which one extreme had the appearance of whole colour.

Variants within the co-dominant tan cheeks and grizzled grey muzzle colour pattern combination were:

- Typical tan cheeks (tan cheeks and upper ears) combined with atypical grizzled grey muzzle (a grey muzzle and no grey on ears). The pattern was therefore a grey muzzle with tan cheeks and upper ears. This could be explained by greatly reduced speckling in the grizzled grey muzzle pattern.
- A grey muzzle with tan cheeks and white upper ears. This could be explained if the tan upper ears of the mahogany pattern were a very dark mahogany colour.
- Grey with tan cheeks and tan/cream upper ears. Again, this could be explained if the grey of the upper ears in the grizzled grey muzzle pattern was greatly reduced speckling.

Overall, therefore, it is likely that grizzled grey muzzled is a distinct pattern in which the muzzle and upper ears are typically grey. The muzzle may vary between whitish and grey, the intensity of the roaning being variable. The upper ears may have a sprinkling of white hairs towards the end of the ear or be grey to whitish all over, including the base.

Variants suggest tan upper ears instead of grey; dark ear tops, and tan on the muzzle. These may be genuine variations or more likely caused by the white in the roaning not diluting, meaning that they remain tan. In the field, and in variable light, it is very easily to mistake a dark mahogany for black.

Nine of these were mahogany in combination with the grizzled grey muzzle pattern.

In the tan cheeks sample, it was found that nearly all (25 or 92.5%) had grey to tan cheeks or upper ears. Of these, 6 (24%) were typical tan cheeks pattern with tan cheeks and upper ears.

Eleven variations were recorded, these being:

- Seven goats (28%) with grey cheeks
- Seven goats (28%) with grey upper ears
- Four goats with both grey cheeks and upper ears
- Five goats (20%) with dark cheeks or ear upper ears

These broke down into 10 variants

1. Grey cheeks and upper ears
2. Grey cheeks and tan upper ears
3. Grey cheeks and dark upper ears
4. Dark cheeks and grey upper ears
5. Dark cheeks and tan upper ears
6. Cream cheeks and tan upper ears
7. Tan cheeks and grey upper ears
8. Tan cheeks and white upper ears
9. Both cheeks and upper ears tan and cream
10. Tan cheeks and dark upper ears

If we accept that tan may dilute to white (possibly due to independent modifiers) the 10 variations could be explained as follows:

- 6 and 9 would be within the typical variation as cream lies within the tan range. Eight may be the upper ear diluting to white. 3, 4, 5, and 10 may be dark mahogany cheeks (of 5 and 10) or upper ears (3 and 4) or weak roaning. Two (grey cheeks and upper ears) may be the tan diluting to white, which would explain also the grey cheeks in 1, 3, 4 and 7.
- Variants 1, 2, 3, 5, 8 and 10 were to be found in goats that were not obviously co-dominant tan cheeks-grizzled grey muzzle pattern. In 2, 4 and 7, the grey upper ears were associated with the mahogany-grizzled grey muzzle co-dominant, so the ears may have been a dark mahogany rather than black.

I found tail colour of some interest, as this varied between black, grey, white and tan. An analysis of my field notes showed a direct correlation between goats with grey muzzles and grey to white tails, and black muzzles and black tails. This led to the conclusion that what I termed the grizzled grey muzzle pattern included roaning on the upper tail.

Overall, the Lynton feral goats showed variations in the shades of tan in their patterning. The eye diamond and legs in the dark striped legs pattern varied from white (which was typical) to a dark tan verging on chestnut. It is therefore conceivable that the roaning on the muzzle, cheeks and upper ears may vary in their intensity between a dark mahogany and white.

The uniformly dark goats with a reddish-tan-black coat were manifestly mahogany colour pattern-thus having tan cheeks and upper ears.

Grey muzzles were typical of the herd, and it was deemed significant that this was found in combination with tan to grey upper ears (95%) and grey to white, very rarely tan, upper tails (100%).

Grey muzzles were found on no pattern black, mahogany, lightbelly and grey with dark legs colour patterns, and so it was reasoned that this was an independent allele related to white spotting, and almost certainly dominant.

It was therefore postulated that roaning (of any colour) on the muzzle, cheeks, upper ears and the upper tail was due to 2 factors (i) the head patterning of the tan cheeks colour pattern, and (ii) an independent dominant allele.

This was initially tested to gauge whether goats exhibited the co-dominant combination of these 2, and this was found to be so. The new allele was therefore named grizzled grey muzzle.

The extent of the patterning was found to be variable; less so on the muzzle, but the ears varied between light roaning on the upper part of the ear tip and a basically white to whitish ear. Cheeks were variable, too- ranging between light (grey or tan) roaning that was difficult to discern, and a bright and clearly demarked cheek patch.

Colour and shade varied a great deal as well, ranging from stark white, through cream to reddish-tan and on to a very dark mahogany that almost blended with black on the cheeks and ears.

Lastly, there was a myriad colour/shade and pattern combinations: 17 in all.

At this point in time, I reasoned that if we conceded that the tan cheeks were a colour pattern, and that the white (grey) may be undiluted and therefore standard tan in the grizzled grey muzzle pattern, then all would have been explained. It would simply have meant that there would be modifiers that varied the intensity of the phaeomelanin roaning.

If, on the other hand, there turned out to be additional independent patterns affecting the head, based upon colour, the main possibilities would then have been:

- Grey cheeks and ears
- Grey muzzle only
- Grey muzzle and tan ears
- Tan cheeks with grey ears
- Tan ears only
- Grey ears only

At the time, these were thought to have been unlikely, the logical explanation being (i) variations in the shades and intensity of tan, (ii) pattern combinations (iii) a variation in the intensity of roaning, along a cline that included hardly discernible speckling.

At this point I was carrying out some research in London's city farms, and came across yet another colour pattern in goats, this being one I had not found in the literature on sheep. Following this, I came across the research that had been carried out at the Macaulay Land Use Research Institute on the inheritance of goat coat colours. At last I had a sound basis for comparing my own research with that of others in to the goat.

5. Anomalies and introductions, why some white goats have an eel stripe, and cashmere production in Scotland to the rescue

During the early days of the study, it wasn't uncommon for goats to be 'dumped' in the valley. On one occasion 2 young males were introduced that had a colour pattern resembling that of the wild bezoar. I had already come across this pattern in a parallel study of the goats being bred by the English Goat Breeder's Association, and I called it 'wild patterning'.

Not long after, a female was left in the valley that had a very strange and interesting patterning. She was, at first glance, like the all-too-familiar Swiss patterning found in both sheep and goats, but there were marked differences. The upper ears were dark, although there were complete facial stripes and white around the muzzle. The forelegs were dark above the knees and hocks, white around the knees and striped below it. The belly was white. Could this have been a co-dominant Swiss pattern-dark striped legs? One problem with this was that the pattern turned up in the herd without any of the goats having a Swiss pattern. This type was called 'white face stripes', and I had hardly a clue as to what its significance was.

Also, in the early days, there were number of goats with strange spotting, although this line died out. At first glance they appeared to be simply 'patched', but the spotting was uniformly rounded, random and often a peculiar shade that almost defied description. Unimaginatively, I called these goats 'big spots', and wondered how they fitted into the spotting locus, if at all.

We have now reached the early 1990's, and I was supplementing my Lynton study with research into the multiplicity of colours and patterns found in the goats kept in London's 20 or so city farms. In one particular farm the goats were of mainly Swiss type- British Toggenburg and British Saanen. Some of the white goats, however, had an eel-stripe and head patterning in the form of complicated facial striping. The latter varied, and I reasoned that this was likely to be the effect of co-dominance between Swiss patterning and the goats that had the eel-stripe. I therefore postulated a colour pattern that I termed 'eel stripe'. In another city farm I came across a goat of Anglo-Nubian type that was all reddish tan with only black facial stripes, belly line and leg striping. At first I postulated a new colour pattern, and one that was not found in sheep. Then I realised that this goat was, in fact, a Bezoar in which the usual white patterning had not diluted to white, leaving all the tan patterning a rich tan colour. Thus, the pelage and the patterning were the same shade of rich tan, meaning that the pattern could not be discerned. This opened the door to consider my eel stripes a dilute extreme (white) of a pattern that would be typically a rich tan in colour. To date, I have not come across one, but the logic holds, meaning that they must exist somewhere.

I had now reached the point at which my own research, in conjunction with a comparison of the inheritance of coat colour and patterns in sheep, had led me to the conclusion that there were at least 10 colour patterns in sheep that had provable parallels in goats. These were:

White

Badgerface or dark belly (from my work with the English Goat Breeder's Association)

Blue

Grey

Lightbelly or black and tan

Grey and tan

Swiss marked

Sooty

Pale cheeks

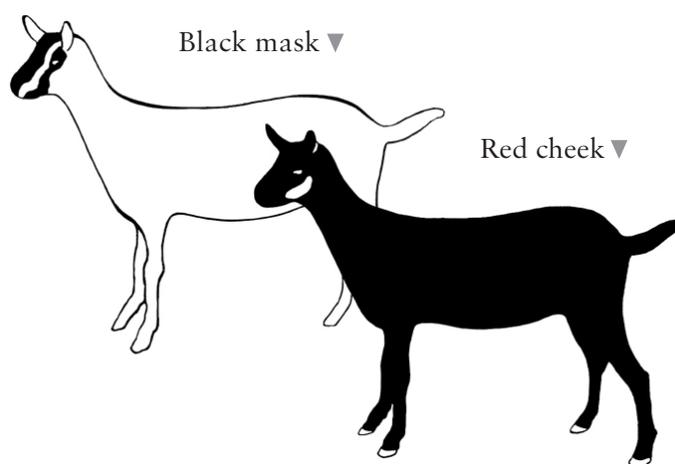
No pattern or non-agouti

Additionally, there were parallels with roan and white spotting. I could not prove grey and tan to be a separate allele at the agouti locus, however.

Additionally, I had identified a further 3 colour patterns in goats that were not recorded in sheep, these being eel stripe, white face stripe and grizzled grey muzzle. There also remained a question mark over grey black legs, as it did not fit easily into any known colour pattern; tan black legs, which may have been roaning or a colour pattern, and big spots.

At this point I came across the research carried out at the Macaulay Land Use Institute, in Scotland. The increasing interest in the production of cashmere fibres had resulted in an examination of colour phenotypes at the Sourhope Research Station during 1990 and 1991. This was published in 1994 (Adaisteinsson, Sponenberg, Alexieva and Russell), although I did not have access to it until much later. The research identified 11 colour patterns in goats, these being:

1. White or tan
2. Black mask
3. Bezoar
4. Badgerface
5. Grey
6. Lightbelly
7. Swiss markings
8. Lateral stripes
9. Mahogany
10. Red cheek
11. No pattern.



This was extremely helpful. Black mask was manifestly my eel stripe and mahogany my tan cheeks as this colour pattern accounted for the reddish tan coats in the Lynton herd.

The illustration of the mahogany pattern actually showed the distinctly tan areas that I had identified as being fawn in Lynton kids, which was further evidence that the reddish-black coat in the herd originates from the mahogany pattern. Lightbelly was my dark leg stripes, but there was no sign of my grey striped legs which was grey and tan in sheep. This suggested that a distinct phenotype in goats was known also as a genotype in sheep. No pattern was my black. My grey black legs was still a puzzle, however. The grey allele on the agouti locus is shown as all grey, meaning that the legs and head are not black. This suggested that the only option available for grey black legs in the Lynton and cheviot goats was grey roan, or roaning on an all black goat. I reasoned that roan may not be lethal in goats, and that the 'wild' allele for non roaning may have been bred out of the Cheviot herd at some time when numbers had fallen very low. The problem remained, however, that grey and grey roan were said to be easily confused. The whole issue was therefore something of a contradiction.

Spurred on by this research, I wondered whether yet more colour patterns in goats could be found. By laying out hundreds of photographs of goats bred by the English Goat Breeder's Association in a sequence of tan patterning, I came to the conclusion that two more, at least occurred. These were similar in some ways to badgerface, but there was more tan patterning on the body. These I called 'saddleback badger face' and 'reverse saddleback badger face'. The difference was whether the tan patterning was to the fore or the aft of the goat.

Following this, a really interesting colour pattern turned up in the Lynton herd. This was a whitish female kid with a distinct black head pattern, some black on the belly and reverse leg striping similar to that of the lateral stripes colour pattern identified at the Macaulay institute. Her dam was a lightbelly (my dark leg stripes) which meant that mum was lightbelly-mahogany co-dormant in phenotype. I knew that lateral stripes in the Macaulay Institute goats came from the Icelandic breed, and was able to establish that a badgerface-lateral stripes phenotype was very similar to the Lynton female kid. This meant that somewhere out there, so to speak, was a laterals stripes-badgerface male that had sired this kid. The problem with this reasoning was that I knew every goat in the Lynton herd, and no such male existed. She therefore remained a mystery goat.

Mystery goat or not, she was very helpful in furthering my journey to identify colour patterns in goats. It happened when I read a breed description of Pygmy goats that included a colour type suspiciously like this very Lynton mystery kid. It was called caramel, and I had not yet heard of it. Googling around to try and find additional information on colours and patterns in the breed, I came across the latest work of Dr. Sponenberg. Much of what was still puzzling me with regard to my own work now became clearer.

6. 'At night all cats are grey' or 'everything seems to turn on grey roan in the lynton herd'

The old French proverb that at night all cats are grey seems to be an adequate summary of the way in which I was always drawn back to a study of roaning in the Lynton herd, and even when I thought, unwisely as it turned out, that the matter had adequately been debated. As my field notes expanded, so did the multiplicity of variations in roan areas covering the head- muzzle cheeks and ears, including an area below the ears- along with the neck and the pelage generally. I was well aware that many variants may have been, in fact, nothing more

than the intensity or otherwise of roaning, or otherwise of no significance whatsoever, but I felt it necessary to consider possibilities based upon converting what I had been observing into theoretical models.

The first issue was that of any possible link between grey neck patterns and the intensity of grey roaning in the pelage.

Having recorded a variety of neck patterns, I concluded that there would be 8 possible combinations, affecting the upper, middle and lower neck, in theory. These ranged from no patterning (a completely dark neck), through 6 variants, to an all grey neck. These may be described as:

1. All dark
2. Grey lower neck only
3. Grey middle neck only
4. Grey upper neck only
5. Grey upper and lower neck
6. Grey upper and middle neck
7. Grey middle and lower neck
8. An all grey neck

Of these, 6 had been recorded in the field: all but 5 and 6.

My expectation had been that there would be a clear link between an all dark neck and an all dark, possibly also lightly roaned, pelage. Similarly, I was expecting an all grey neck to link with a pure grey, also possibly mahogany grey, pelage. If this were so, then intermediate neck patterns and pelage patterns, in relation to the intensity of roaning, were also expected to form some sort of a cline. Not so.

The only pelages that linked with an all dark neck were most certainly all dark and flecked, but an all dark pelage was also linked to neck patterns 3, 4 and 8, eight being all grey. Likewise, a lightly flecked pelage was linked with neck pattern 3 and the all grey 8. The blackish grey pelage was linked to neck patterns 3, 4 and 8; whilst mahogany grey was associated with neck patterns 2, 3, 7 and 8. Pure grey was linked to 3 and 8. Thus, an all grey neck was associated with all 5 pelage patterns, from the extremes of a plain coat to pure grey: whilst neck pattern 3 (grey middle neck only) and neck pattern 7 (grey middle and lower neck) were also associated with all 5 patterns. There may have been a pattern to the patterns, so to speak, but I failed to find it. Of course, the potential to exhibit more neck patterns in the 5 pelage patterns than were recorded may have existed, in which case the herd was too small in number to realize this.

I also looked for any link between grey below the ear and either grey neck pattern or grey ears linked to grey muzzle. As a casual observation, it did seem that a grey middle neck was an extension of the grey around the ear base, which could also have been true of the more extensive grey neck patterning that involved the middle neck. Sampling 93 goats, 56 had grey around the base of the ear, 29 were dark at this point, and 8 had tan around the base of the ear.

Of the 56 goats with grey below the ear, 51 (91%) had grey necks, whilst 5 had dark necks. Thus, grey around the base of the ear was typically, but not universally, associated with grey on the neck. In relation to neck patterns, grey around the base of the ear was linked to patterns 1, 3, 7 and 8. All 4 were neck patterns with a grey middle neck. Of the other patterns (2, 4, 5, and 6), only 6 had a grey middle neck, the others being dark at this point. The results did not seem to fit a clear pattern, as in patterns 1, 3 and 7 the area around the base of the ear can be either grey or dark.

Tan around the base of the ear was also inconsistent. In 1 goat, the tan base linked to a tan/grey upper neck and grey middle and lower neck. In another 2, the base around the ear was tan/cream along with the whole of the neck. In 1 other goat, the tan at the base of the ear was linked to a grey middle neck (neck pattern 3), whilst in 4 other goats, the tan at the base of the ear was associated with an all dark neck.

In looking at the link between a grey ear base and grey muzzle, the results for 97 goats were as follows: 70 had a grey base to the ear and a grey muzzle; 19 both a dark ear base and muzzle; 5 a dark muzzle and tan ear base, and 3 a grey muzzle and dark ear base.

It was therefore concluded that a grey muzzle linked to grey ears, including the area around the base. It was also concluded that with the commonality of a grey muzzle in association with grey on the neck, there need not be a firm link between a grey ear base and grey neck patterning.

Linking head patterns in the greys with pelage was also confusing. It was theorized that a light grey head would align with the pure grey or grey mahogany pelage; whilst an all black head or black head with a grey muzzle would align with the blackish greys. Not so, again. An all black head was found in all 4 of the grey roans (pure grey, mahogany grey, blackish grey and mahogany blackish grey). This was also the case with a black head and grey muzzle. A black head with grey muzzle and cheeks was also found in all 4 pelage types. However, a grey head with black forehead and face was recorded only in the pure greys and mahogany greys; a grey head with only a black forehead in the mahogany blackish grey, and an all grey head in the extremes of the pure grey and the mahogany blackish grey. It was therefore very difficult to align head patterning in the greys, along a cline, with the intensity of roaning

Lastly, when focussing on grey roan, 3 possibilities were considered that might explain the range of roaning encountered in the Lynton herd. These were:

1. Mahogany pattern, agouti grey and roan present
2. Mahogany and agouti grey only present
3. Mahogany and roan only present.

The possible base colours in the herd were considered to be black (no pattern) mahogany/black (mahogany pattern) and white/black (agouti grey pattern) at the agouti locus.

If mahogany pattern, agouti grey and roan were present in the herd, then pure grey could be explained as agouti grey and roan; mahogany grey (which is grey with additional tan roaning) by way of a mahogany pattern-roan cross; blackish grey as a dark roan; and mahogany blackish grey as a mahogany pattern-dark roan cross. If only mahogany pattern and agouti grey were present, then it is difficult to explain the blackish greys. If only mahogany pattern and roan,

on the other hand, are present, then all for pelage types in the greys can be explained. The result is that to cover the 4 pelage types, agouti grey need not be present although roan would appear to be needed.

One difficulty with this is that although black seems to be present in blackish grey, uniform black does not seem to occur.

The general conclusion, when considering the grey roans, was that it was hardly possible to define an association between the grey head and neck patterns in relation to either each other or the pelage types. It was considered a given, at the beginning of the analysis, that roaning in the neck and body regions would be similar, which assumed an overall roaning, and that the head patterns would also be in keeping with this. Nothing seemed to work out however. As it turned out, a focus on grey provided good additional information for recognition charts, but not what was hoped for in terms of the inheritance of coat patterns.

The one compensation, however, was that my disappointment coincided with the discovery of the 'Sponenberg factor'.

7. The Sponenberg factor

When I began my research, there was no clear evidence of colour patterns in goats, and characteristics such as eel and face stripes were thought to be inherited independently. Over time, however, I was able to clarify colour patterning, co-dominance in the phenotype and a number of issues around piebald or white spotting. The work on colour inheritance in sheep was a huge boost to my understanding, along with the research carried out into colour inheritance in goats in the early 1990's. But, the last pieces of the puzzle fell into place when I came across the updated work of Dr. Sponenberg.

A total of 25 colour patterns, located on the agouti locus, were identified. Along with this, there were 13 variations of 'white spotting'.

What I had researched as saddleback badger face and reverse saddleback badgerface have been designated peacock and repartida.

The female kid that I had thought of as being a lateral stripes-badgerface co-dominant phenotype turned out to be a colour pattern named caramel that is quite common in American pygmy goats. This helped only in terms of identification, as the problem of how a caramel male got near to the Lynton herd remains a huge puzzle.

My face stripes is, in actuality, a colour pattern now known as striped lightbelly, and I have since established that this colour pattern was found in the early British Alpine breed.

Turning now to white spotting, 3 types of white patterning, all distinct from random spotting or piebald, have been identified. These are distinct from 'random spotting', which I called white spotting. One of these is the same as my belted and actually called belted! A second, called Cou noir, has the head and forequarters black and the remainder of the body white. Both these are in keeping with my hypothesis that there are distinct areas of the body that

alleles control for white replacing the base colour in a block. Whether or not the 'broken up' pattern of the Bagot goat is Cou noir with the additional allele for random spots, or Cou noir with modifiers for smaller areas of white elsewhere to random spots is as yet unclear, but I am working on it.

My hypothesis that the white forehead patch so typical of Lynton goats was inherited separately turned out to be accurate. It is almost universal in Nigerian pygmy goats and is a dominant as I predicted. It is often associated with a white tip to the tail, something I missed completely in my own analysis.

My big spots were actually a separate allele, as I had speculated, but called moon spots.

Grizzled grey muzzle characteristic really does exist. It is known as frosted, is common in Pygmy and Nubian goats, and results in the nose and ears being roan to nearly white. As I predicted for grizzled grey muzzle, it is a dominant. In Pygmy goats, the degree of roaning can be quite variable, at times very difficult to discern, and this seems to be in keeping with the difficulties I had in establishing the extant and variability of my own grizzled grey muzzle.

Lastly, there is the grey range. A grey that appears to parallel 'blue' in sheep has now been identified in Pygmy goats, meaning that the coat is grey and legs are black, but there is additional patterning in relation to an eel and shoulder stripe. This is called agouti grey (Aga). There is also a striped grey, which is effectively a grey Swiss pattern (Asg), a grey (Ag) and a grey roan.

With an enlarged group of alleles in the grey patterns, one would think that the task of identifying my 'grey black legs' with an established pattern would be made easier. Not so, it being suggested that the legs and head may be 'somewhat darker'.

After reading the Macaulay study I had researched the grey pattern world-wide, finding many examples of breeds that were concolourous grey. Was it possible, therefore, that the grey allele was very variable in its coverage as well as its density?, meaning that it was possible for the grey colour pattern to be either uniformly grey or grey on the body and neck but black on the head and legs. Alternatively, my theory regarding co-dominance in the roan coats of the mahogany colour pattern and roaning at the roan locus was an equal argument for grey blacklegs being a black roan, with the mahogany grey goats being a mahogany-black roan. On balance, I now favour the latter, which would mean that the Cheviot goats of the College Valley went down a genetic cul-de-sac in which the potential for non-roaning was eliminated.

A query remains, however. Does Hard's rusty black exist as a variant of black, or can this be accounted for by the mahogany pattern? The Old Irish goat was often described as being a rusty black, but there is no additional evidence as to whether or not they had tan cheeks as well.

One interesting follow-up to a better understanding of the characteristics of colour patterns has emerged. A re-examination of my field notes has shown that there are some anomalies in the rules governing co-dominance. Obviously, patterns combine in the phenotype, but the light areas from both patterns will dominate. This means that black will only occur in those

areas where it is found in both patterns. Whilst this is generally true, I have come across a number of examples in the Lynton feral goat in which white ears occur in grey black legs, and black ears in the light belly pattern. Theoretically, this should not be possible. I used to be quite confident that I could discern the colour pattern of a goat lying up in bracken by the colour of its ears alone, but not any more.

Lastly, the genetics of colour patterns has proved to be of interest in tracing the history of British goat breeds. The early imports of Toggenburgs, for example, did produce some black kids as opposed to the desired light brown. This is due to the fact that Swiss pattern in goats is black with white patterning, but that the recessive brown allele at the Brown locus changes anything that is black on the goat to brown. The Toggenburgs is therefore brown Swiss patterning rather than black. At the time of the first imports, Swiss goat breeders could only claim a subsidy on 'pure breeds', the Toggenburg being deemed to be brown. Black kids occurred, but were always destroyed. In similar vein, the early English breeders of Toggenburgs destroyed any black kids that occurred in the early imports and their immediate descendants.

Also, a study of the early British Alpine breed has shown that a significant number were not Swiss pattern at all but striped lightbelly or what I had termed 'face stripes'. Additionally, the early British Alpines were sometimes roan, but the roaning was hardly discernible. A good example of this was the famous stud goat Prophet of Bashley, who was not Swiss pattern, although mistaken for such, and bred as a grey. During a trawl of the early history of the breed, including the study of many old photographs, I found that white bellies were quite common, being found in prize-winning goats as late as the 1940's. The early breed description allowed for this, and I assumed that such goats would always have been the co-dominant Swiss pattern-lightbelly cross. But the presence of white bellies as late as the middle of the last century in the breed meant that this could not have been the whole story. In studying the photographs, I am pretty well convinced that there is a separate allele at the agouti locus for a white-bellied Swiss pattern, which I call, simply, 'light belly Swiss pattern'. As time goes on, more detective work will show up other interesting aspects of goat history and development in relation to colour patterns

End piece

When I begun my study of the colour and markings found in the Lynton feral goat, and expanded this to include the pot pourri of breeds and types to be found in London's city farms, the literature I had had to hand suggested that colours were inherited in terms of dominants and recessives, and additional features, such as leg and eel striping, face stripes and white bellies, were inherited separately. It didn't take me long, however, to conclude that something was seriously amiss with the published literature. Proceeding was largely trial and error, even so, and sometimes entailed waiting for the right kid to be born to prove a cherished new theory. One major difficulty was that although there was a dawning of the idea of both distinct colour patterns and co-dominance from my research, I still, for a period of time, tried to fit my data into the established view of goat colour genetics. Stepping outside of this was difficult, but once I embraced these ideas, everything seemed to fit into place. It all seems so simple and logical now, but that is only hindsight.

Examples of colour patterns in the Lynton feral goats:



▲ Grey Lightbelly Lynton female

◀ Mahogany Lynton female