Module 13
Diet, Feeding and Animal Welfare

Lecture Notes

Slide 1:

This lecture was first developed for World Animal Protection by Dr David Main (University of Bristol) in 2003. It was revised by World Animal Protection scientific advisors in 2012 using updates provided by Dr Caroline Hewson.

Slide 2:

When we consider diet and animal welfare, we typically think of the functioning aspect of welfare – that is, how diet affects health and production.

However, as we have seen in some of the other lectures about different species, **how** we feed animals and **what** we feed them also affects the other two aspects of welfare: animals' feelings and the extent to which they can perform behaviours that are important to them.

Remember that, in general, veterinary medicine has tended to overlook this last aspect. However, this behavioural aspect of welfare can be as important as physical functioning and feelings (and therefore mental state) and all aspects are interrelated. In the following discussion we will try to incorporate all these aspects.

We will end the lecture by looking at how to maximise welfare when feeding animals.

Slide 3:

We start with hunger and feeding.

- Hunger is a feeling, and prolonged hunger can cause suffering. For that reason, the absence of prolonged hunger and thirst is the first of the four main areas of welfare assessment that we cover in several of the other modules.
- Hunger is related to appetite which is coordinated by the hypothalamus. The appetite centre there is affected by many internal cues, including body temperature, mental state, neural inputs from the gastrointestinal tract, and blood-borne metabolites such as glucose and urea. The appetite centre is also affected by external cues including the smell of food.
- Clinically, you will see this in your patients: inappetence is often a clinical sign, as animals typically lose interest in food if, for example, they are pyrexic, frightened, in pain, or have high levels of blood urea or liver enzymes because of pathologies in the kidneys or liver.

- In the wild, both carnivores and herbivores encounter variability in the availability of food.
- Herbivores may experience prolonged hunger and have periods of low food intake because predators keep them from areas of good forage, or because of the weather, e.g. drought.
- Similarly, carnivores may also experience prolonged hunger as they may not always be able to find prey.
- However, being hungry also gives animals something to do, i.e. looking for food, finding it, killing it (carnivores) and then eating it. Also, research on farmed pigs indicates that the anticipation of finding food is as pleasurable as consuming it. This is the same as our experience as human beings when we are hungry.
- The normal feeding behaviour of most species of animal involves periods when the animal seeks out food and eats it, and periods in between when he or she performs other behaviours, as far as the environment permits this.
- Within each bout of feeding, the amount that an animal ingests may vary depending on his/her genetics and on how the food is presented in the environment. However, his/her overall feeding pattern will be largely independent of the quality of the food, or the genetic tendency of the animal to grow quickly. Therefore, even though some farm animals are bred to grow quickly and may be chronically hungry in adult life, they do not spend all their time looking for food.

Slide 4:

Feeding behaviour has two components.

The first component is 'appetitive'. Here, the animal seeks out the object that is needed in order to satisfy the underlying motivation (e.g. in the case of mating, the appetitive component is the courtship ritual; in the case of feeding, the appetitive component is acquiring the food in the first place – pigs root in order to smell and uncover the food, dogs sniff the scent of prey, neonates suck on the teat).

The second component is 'consummatory'. Here the animal performs the behaviour that satisfies the life-sustaining (or health-sustaining or comfort-sustaining) motivation that drives the entire behavioural sequence. In the case of mating, the male mates with the female. In the case of feeding, the animal takes the food, chews it (if necessary), and swallows it.

Among most systems for domestic animals, the nutritional focus is on the consummatory part of the feeding behaviour: in order to live, the animal must ingest the food. By feeding animals, we satisfy their hunger.

However, even though eating may allay animals' hunger, it often does not provide sufficient feedback to satisfy the appetitive component of their feeding motivation. This can give rise to frustration, which may be manifested as behavioural and physical abnormalities such as stereotypic behaviours and gastric ulceration, as we shall see later on.

Slide 5:

As we consider the connection between feeding and hunger and other aspects of animal welfare, note that human factors are balanced against the animals' welfare. The feeding regimen can therefore depend on the number of animals to be fed, the time available to feed them, the cost of labour, the cost of the feed, the economic value of the animal, and the owner's income and profit margins. These factors may affect welfare adversely. For example:

- animals may be malnourished if they do not have high economic value or if the owner has little money to feed them
- conversely, animals may be fed well with regard to physical functioning, but the cost of labour or their housing may result in a feeding regimen that does not permit them to express the full range of their feeding behaviour – so they may not feel prolonged hunger, but they may suffer from chronic frustration
- the animals' non-financial value may also affect the feeding regimen. This is most notable in the case of some companion animals, whose owners may over-feed them as an expression of affection
- over-feeding animals is a financial cost to owners, but a non-financial benefit because it increases the owners' pleasure. It is also pleasurable for the animals. However, it predisposes the animals to diseases such as diabetes mellitus and osteoarthritis which create further financial cost to the owner and reduced physical functioning and suffering for the animal.

Slide 6:

The two main types of feeding regimen for domestic animals are *ad libitum* feeding and dietary restriction.

Ad libitum feeding is the unlimited access to food. This allows animals to follow their natural pattern of eating in bouts. This type of feeding is standard in a number of situations:

- growing broiler chickens and growing pigs in intensive systems. Those animals are from genetic lines which have a rapid growth of skeletal muscle, which enables them to reach market weight in a relatively short time. This rapid growth is accompanied by a large appetite, and *ad libitum* feeding is an efficient way to enable the animals to maximise their growth rate
- laboratory rodents are commonly fed *ad libitum* as this is labour-efficient
- some pet owners feed their animals *ad libitum*.

Laboratory rodents and companion animals may be at risk of obesity, depending on how energy-dense and palatable their food is.

Obesity is the presence of excessive adipose tissue that presents a risk to health. For animals this assessment is based on a combination of body weight, measurements of the trunk, and subjective scores of the subcutaneous and intra-abdominal fat using standardised five- or seven-point body condition scoring (BCS) systems.

Obesity can lead to many problems, including:

- health disorders, because of the added physical requirements that it places on the heart and the musculoskeletal system, and because adipose tissue has endocrine effects. For example, excessive adipose tissue predisposes other tissues to insulin resistance, which results in diabetes mellitus
- reduced longevity (obesity is deliberately created in some laboratory rodents in order to study the mechanisms involved).

You can see from this that *ad libitum* feeding of high-quality food can reduce physical functioning and cause suffering.

The second type of feeding regimen, dietary restriction, is intended to prevent these problems.

Slide 7:

Dietary restriction may be quantitative or qualitative, or a combination of both.

With 'quantitative' restriction, high-quality food is given, but in restricted amounts. This is commonly done with breeding stock of pigs and broiler chickens, and in laboratory studies of obesity in rodents (typically rats).

The first way to restrict the amount of food consumed is only to provide a percentage of what the animals would consume if they ate *ad libitum*. The slide shows the approximate percentages of restriction that are typical for the breeding stock of pigs, broilers, and laboratory rodents.

Another way to restrict the amount ingested is to restrict the time during which food is available.

A third way is to make access to food more difficult, e.g. by providing complex feeders that the animal has to manipulate in order to access the food.

Quantitative restriction can adversely affect welfare in the areas of feelings and performance of important behaviours because:

- it may not produce a feeling of satiety, so animals still feel hungry. This is a major concern with the breeding stock of broilers and pigs. For example, there is evidence that ongoing hunger affects the ability of broiler breeders to learn tasks, even when the reward for learning is access to more food
- rodents used for studies of dietary restriction may be housed singly in order to ensure they receive the exact amount of food required for the experiment. However, rats and mice are social animals and housing them singly can be distressing. If rats are group-housed on quantitative dietary restriction they may show high levels of aggression to other rats

- if the animals are on quantitative dietary restriction and their environment is also restricted they may be unable to relieve their remaining feelings of hunger by performing species-typical food-seeking behaviour. This can predispose them to redirect their food-seeking behaviour, which may in turn become stereotypic. Such behaviours are common in sows kept in crates and in broiler hens, as we shall now discuss.

Slide 8:

We have noted that the breeding stock for broilers and pigs cannot be fed to appetite for reasons of cost and animal health.

In particular, a broiler breeder hen's abdomen cannot accommodate a lot of food in the gut because the egg in the reproductive tract already takes up a lot of space. If these birds have a very full gut as well, this predisposes them to prolapse of the vent and vent-pecking.

For sows, feeding to appetite would lead to obesity which would in turn reduce fertility, increase strain on the musculoskeletal system and result in joint pain, which would increase the risk of the sow lying on her piglets.

Because of these real welfare problems relating to health and functioning, sows and broiler hens in intensive production systems are on quantitative dietary restriction: they are either fed every other day, or they are fed a reduced amount each day. Consequently, they are thought to feel chronically hungry, especially in light of their naturally large appetites.

Under those conditions, some sows and caged broiler breeders show redirected or stereotypic behaviours that are related to eating. They show these behaviours as they hear the noises that signal the arrival of food, and after eating.

- Sows bar-bite and head-weave, root and vacuum chew.
- Broiler breeders pace and walk before feeding and afterwards they also show a lot of oral behaviours – pecking at the feeder and at the litter if present.

Showing these behaviours before food arrives is thought to reflect hunger-driven, food-seeking behaviours. The animals then consume the food very quickly. However, they probably still feel hungry because the amount eaten is insufficient to provide negative feedback to the appetite centre in the brain and reduce their motivation to seek food.

Consequently, the redirected and stereotypic behaviours shown after eating appear to reflect elements of the food-seeking behaviour that they would show under natural conditions of hunger (rooting, chewing and pecking).

The presence of the behaviours may be adaptive and it may be that the animals who **do not** develop the behaviours are actually suffering more. Nevertheless, the behaviours also point to a very constrained environment.

Given all these welfare challenges of quantitative dietary restriction, qualitative restriction would seem preferable.

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With 'qualitative' dietary restriction, food is available *ad libitum* but the nutritional quality of the diet is restricted. So we can see that the animal's essential nutritional needs are met, but the diet is otherwise relatively high in non-digestible material which promotes gut fill but does not contribute to energy intake.

Qualitative restriction seems to be an effective way to prevent obesity and also minimise behavioural signs of distress in ruminants and other herbivores such as rabbits and horses. This is because herbivores naturally spend much of their time selecting and grazing on plant material.

High-fibre diets are also available commercially for dogs, cats, pigs, broilers and laboratory rodents. However, the concern with those species is that, unlike herbivores, under natural conditions hunger would motivate them to spend a relatively long period of time finding their food and only a short time eating it. So, simply providing them with a bulky diet may still not adequately satisfy their motivation to find food, and this may cause strong feelings of frustration.

You can see that quantitative and qualitative dietary restriction each have a logical rationale but that they can create other welfare concerns. Consequently, researchers' views differ about the two methods of restriction.

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Some researchers argue that although qualitative restriction reduces the performance of redirected feeding behaviours and stereotypies, the longer ingestion involved with qualitative restriction is still a behaviour that is motivated by hunger. Therefore, in both quantitative and qualitative dietary restriction, animals are responding to ongoing hunger, which is a welfare concern.

Other scholars note that, under natural conditions, the supply of food varies in amount and in quality, so animals are adapted to eat more low-quality food. Providing them with this *ad libitum*, in qualitative dietary restriction, allows them to regulate their intake according to fundamental internal cues. Therefore qualitative restriction is preferable to quantitative restriction.

Similarly, because animals are adapted to lay down adipose tissue at times when food is plentiful, quantitative restriction conflicts with a fundamental metabolic adaptation and may create a particular experience of metabolic hunger. Again, qualitative restriction would seem better for welfare than quantitative.

On the other hand, anticipating the discovery of food is an important source of pleasure in carnivores and omnivores. Therefore, anticipating the arrival of restricted amounts of high-quality food, as in quantitative restriction, may enhance their welfare.

You can see from this that identifying the best feeding regimen for animals is not necessarily straightforward as it depends partly on which aspect of welfare is emphasised – physical functioning, feelings/mental state or natural behaviours.

We shall now look at other aspects of hunger and animal welfare.

Slide 11:

There are two other common welfare problems relating to feeding farm animals in some systems.

The first concerns the practice of 'forced moulting' in laying hens (i.e. hens who produce eggs for human consumption).

In some countries hens may be subject to a 'forced moult' at the end of their laying cycle. This is when feed, water and sometimes light are severely restricted for up to two weeks, then restored so that the birds resume laying.

The food restriction causes feather loss (hence 'moult') and subsequent regrowth. The practice maximises egg production per bird and can be economical for the farmer because of the pricing structure of the local market.

The principle behind forced moulting is that in the wild some birds naturally restrict their food and water intake before coming into lay. However, a forced moult imposes severe restrictions on hens. Also, because of the underlying economic cause, it is typically used as part of the husbandry of caged hens who do not have the space or facilities to express their motivation to eat (e.g. by foraging).

Consequently, forced moulting is illegal in several countries on the grounds of animal welfare.

The second issue concerns metabolic hunger in high-producing dairy cows. Over the last 40 years, genetic selection for high production has increased the yield per lactation from approximately 3,000 litres in the Friesian, to up to 18,000 litres today in Holstein and Holstein Friesian crossbreed cows. That can mean an average of up to 50 litres per day, for around 320 days of the year.

On grass a cow can only eat enough to produce 25 litres of milk each day. However, her inherent metabolic drive is to produce 50 litres a day. This makes her hungry if she only eats grass, and it causes her to lose weight.

To avoid this, she needs additional concentrated feed. However, her natural tendency is to graze instead, so to ensure she has enough room in her to contain the concentrated feed needed for high milk production it becomes more cost-effective to keep her inside all the time.

Even then her inherently high milk production means that she is likely to be hungry some of the time, while also having a very full gut, so her capacity to keep eating is limited. Also, she needs time to lie down and digest the food as well as simply to lie down and rest. These needs may conflict, i.e. she may want to eat in order to diminish her hunger, while having a full gut, while needing to stop eating and lie down.

Therefore, in some systems the highest-producing dairy cows may experience a combination of hunger and exhaustion for much of the time.

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In the instances we have looked at so far, the nutritional requirements of the different species are well known by their caregivers, and the question for them is how to meet the animals' nutritional needs while preventing obesity or excessive weight loss, and maximising production.

Another category of welfare concern is where the caregiver lacks knowledge of dietary requirements and does not feed enough food of sufficient quality, and the animals become thin and lack essential nutrients.

This problem is widespread in parts of the world where there are limited veterinary services. For example, a study of dogs in two rural areas in South Africa where there were no veterinary services indicated that many dogs were thin because they were not fed enough protein.

Many working equids are also likely to experience prolonged hunger because they are not fed enough for the work that they do. Exacerbating this, during periods when they are not working they may only be fed a low-maintenance diet, meaning they are weak when the working season starts again. This can predispose them to disease and other welfare problems.

For example, in a study of ~10,000 working equids from nine developing countries (including Guatemala, India and Ethiopia), body condition score predicted other aspects of welfare. That is, thinner animals were more likely to have skin lesions, gait abnormalities, etc. than animals of normal weight.

A small minority of psychologically disturbed people hoard animals in large numbers but are unable to feed or care for them. Often those animals are starving.

Other owners may deliberately starve their animals in order to be cruel to them. As veterinarians, it is very important to be aware of animal neglect and cruelty, partly because research suggests that animal abuse is an indicator that other members of the owner's family are also suffering abuse – usually his/her partner/spouse and children.

In countries where animals are protected by law, veterinarians who encounter animals who are under-nourished due to owner ignorance or suspected cruelty, and who cannot ensure that owners will feed their animals a sufficient amount, should refer the case to the authorised animal protection groups – usually the local department of agriculture [livestock] and/or the local animal welfare organisation. Module 5, on legislation, and Module 30, on human–animal interaction, look at this more closely.

If presented with a severely starved animal, it is often best for their welfare to euthanise rather than to invest large amounts of money in trying to restore them to health, as death is likely in any case.

Slide 13:

You can now see that as a vet in practice you will have clients who will use different feeding regimens for different reasons.

Note that, in addition to feeding regimen, other more clinical factors can make animals hungry despite a balanced diet. Briefly, they include:

- parasites – gastrointestinal (GI) parasites cause inflammation of the GI tract and may absorb much of the digested food there. Parasites may also prevent the absorption of food, by covering up the villous surface of the small intestine. Depending on the parasite load, the parasite itself, and the stage of its life cycle, affected animals may not have diarrhoea. However, they may be thin and have an increased appetite
- maldigestion – animals who are unable to digest their food are hungry. A classic example of this is exocrine pancreatic insufficiency which is seen in dogs. Another example is when the teeth of herbivores are in poor condition so their food cannot be not masticated enough (e.g. horses, rabbits)
- malabsorption – here, the animal cannot absorb the digested food. Most commonly this is caused by inflammation or neoplasia of either the small bowel or the large bowel, or both. Because many farm animals do not have long lives, diseases of malabsorption may not be seen in these species. However, these diseases are seen more often in dogs and cats
- malutilisation – this happens as result of metabolic diseases such as diabetes mellitus. As noted earlier, obesity (over-feeding) predisposes animals to diabetes mellitus.

Slide 14:

When we consider the effect of food and feeding on welfare we also need to consider thirst.

The sensation of thirst is thought to be regulated in the walls of the third ventricle of the brain in response to endocrine, osmotic and neural factors. Some causes of thirst include insufficient water and water loss through disease or sweating. The pig in the picture is drinking from nipples which always supply fresh clean water.

Insufficient water: as discussed above in the section on hunger, a small minority of owners may neglect to provide any water to their animals. However, it is more common that there are problems with the water delivery systems, e.g. freezing in cold weather.

In the case of broilers water is usually provided by nipple-drinkers. The drinkers are raised up to prevent the birds from banging into them as they grow. However, broilers are also prone to lameness because of the rapid growth of their muscles compared to their bones. Lame broilers may not be able to reach the raised nipple-drinkers and will die of dehydration if they are not removed and euthanised.

For pigs, a lack of water can become very serious very quickly, as they develop hypernatraemia (salt poisoning) which rapidly causes death by dehydration.

In the case of veal calves, research has indicated that calves raised on an all-milk diet would drink water if it was available. Providing water as well as milk reduces undesirable oral behaviour such as sucking that is not related to feeding.

The provision of water to veal calves is also associated with reduced prevalence of ulcers in the fundic region of the abomasum (i.e. the main body of the abomasum), but does not affect the occurrence of ulcers in the pyloric region (the distal end of the abomasum).

Calves on an all-milk diet who do not receive water are not dehydrated. So, water seems to provide environmental enrichment to veal calves and also reduces behavioural and some physical signs of stress.

Working equids are most typically found in hot countries, and need more water than horses in cooler countries. However, in a study of 4,903 working equids in five different, hot countries, approximately 40–50 per cent of the animals were dehydrated using the skin pinch test.

Slide 15:

Other, clinical, factors can make animals thirsty, despite access to water. Briefly, these include:

- stomatitis – infectious diseases that cause stomatitis (e.g. feline calicivirus in cats, foot and mouth disease, *peste des petits* in ruminants) and other diseases that cause difficulty in swallowing (e.g. megoesophagus; oesophageal obstruction) may prevent the animal from drinking enough water, and result in thirst
- metabolic/renal diseases – various diseases can cause increased thirst in animals (e.g. diabetes mellitus, renal disease, hyperthyroidism, hyperadrenocorticism). The resulting polydipsia is accompanied by polyuria
- GI disease – loss of body water most commonly occurs due to diarrhoea or vomiting. Both of these conditions directly cause a loss of water. They also produce electrolyte imbalances which lead to changes in the balance of water contained in the intracellular and interstitial fluids, and in the blood. Where the animals also suffer malaise, they may be unwilling to drink
- excessive sweating, in very hot weather. Initially this increases thirst. However, if the heat is extreme and animals are not given shade and sufficient water, they lose so much sodium via sweat that this suppresses thirst. In order to restore thirst and the normal physiological means of controlling body water, it is necessary to restore the animal's sodium balance first. (Providing shade and ample water is particularly important for draught animals in hot weather. The picture shows a donkey in Ethiopia: the person in the picture has an umbrella to shade him, but the animal is in full sun
- pathological thirst – this is not common, but can be caused by under-secretion of antidiuretic hormone or lack of sensitivity of the kidney to that hormone. The condition is known as diabetes insipidus, and affected animals drink excessively large amounts of water.

Slide 16:

So far, we have looked at the issues surrounding the ingestion of food and water and how these may be affected by the animals' husbandry and health.

We shall now consider how diet can affect other aspects of animal welfare. First, we shall look at how diet affects physical comfort. We shall start with body temperature.

Under-nourished animals are thin and lack the insulation of body fat. Therefore, they have to use up more metabolic energy to maintain body temperature. This increases their demand for food. If they are unable to maintain their body temperature they may become susceptible to infection. Also, if they develop disease – infectious or otherwise – for other reasons, they are more likely to become 'cachectic', i.e. to suffer catabolism of skeletal muscle.

Conversely, overweight animals can suffer in hot weather because the fat on their bodies retains heat within the body. Obese dogs may pant almost continuously in hot weather; panting also generates heat, which is likely to add to their discomfort. Obese cats may have difficulty reaching back to lick their torso in order to cool down by the evaporation of saliva.

Diet also affects physical comfort in terms of the amount of subcutaneous adipose tissue. Very thin animals are prone to sores and skin infections because their bones have no fat cover and little muscle cover. This makes the bones protrude, and the overlying skin is easily rubbed by harnesses or by the floor on which the animal is lying.

The third way in which diet affects physical comfort concerns ease of movement.

Obese animals may have difficulty supporting themselves when they urinate or defecate. Very fat cats are often unable to groom themselves properly.

Meat birds (broilers and turkeys) have been selected to grow quickly if they are fed *ad libitum*. Under this regimen their rapid growth predisposes them to joint and tendon problems, which restricts their movement and makes it difficult for them to move to drinkers and feeders. The picture shows a lame broiler.

With laying hens, their high egg production (~300 eggs per bird, per laying year, in cage systems) depletes body calcium. This is because it is impossible to supply enough calcium for eggshell production in their diet without creating other dietary imbalances. Moreover, it is impossible for the birds to absorb enough calcium dietarily, for eggshell production. Consequently, the birds utlilise calcium from the skeleton, especially the long bones. This weakens the bones, i.e. causes osteoporosis. The problem can be partly offset by light stimulation before the start of lay. However, osteoporosis tends to be prevalent at the end of lay because of the chronic demand for calcium (Scott, 2011). As a result, these birds are prone to osteomalacia and osteoporosis, resulting in mortalities and in fractures when they are transported and shackled for slaughter.

In addition, the inability of laying hens to either land on perches or to descend from them (in perchery/free-range systems) gives rise to a high prevalence of fractures of the keel bone.

These diverse examples illustrate how an animal's diet can affect his/her physical comfort.

Slide 17:

How we feed animals and **what** we feed them can predispose them to disease and pain.

As vets in practice you will encounter animals who are diseased because of lack of vitamins and minerals. Such deficiencies can also cause pain and injury. Examples are:

- fractures due to deficiencies in Vitamin D or calcium – animals who are deficient in Vitamin D (e.g. dogs who are kept in the dark and fed a phosphorus-rich diet of raw meat and wheat-bran) develop rickets and are prone to fractures
- calcium deficiency in hens – we saw earlier that laying hens cannot obtain enough calcium to meet their requirements so they are prone to osteoporosis and consequent fractures
- taurine deficiency in cats – cats who are deficient in taurine develop cardiomyopathy, which may lead to the development of blood clots at the caudal aorta; the resulting lack of blood supply to the hind legs is extremely painful. Most commercial cat food contains taurine so signs of deficiency are rare now
- mineral deficiencies, such as hypomagnesaemia – young grass, particularly when it is nitrogen-rich, is low in magnesium and so when cattle or sheep are put on it they may develop hypomagnesaemia. The condition causes tetany ('grass staggers'), which is fatal if not treated promptly
- deficiencies in selenium or copper in local soil – this means grazing animals need mineral licks or other supplements. Animals who are deficient in minerals may show pica: they will eat non-food items such as their stools or the soil, which may give rise to digestive upsets
- iron-deficiency anaemia in veal calves – this is induced by the traditional milk-only diet with no forage. This and results in the highly prized 'white' meat. The feeding of milk-only diets to calves became illegal throughout the EU from 2007 for calves aged over eight weeks
- predisposition to obesity and deficiencies in vitamins and minerals – pet birds and small pet mammals (such as guinea pigs and rabbits) are often fed highly palatable but unbalanced mixes of loose seeds and cereals.

Slide 18:

A further problem that you will encounter in practice is overfeeding.

Overfeeding companion animals is a growing problem. Contributing factors are the marketing of highly palatable food and owner ignorance.

For example, studies of feral cats indicate that when supplying their own food by predation, they will have 8 to 16 meals a day: they eat small rodents, birds, insects, and lizards (in some countries). The approximate calorific requirement of an active cat is ~60 kilocalories per kilo of bodyweight. A 4 kg cat requires ~240 kcal per day. The approximate bodyweight of a mouse is ~ 30g and one would supply the cat with approximately ~30 kcal. You can see that, in order to ingest enough food each day, and depending on the availability of prey, the cat would eat a lot of small 'meals' in one day.

A lot of cat owners provide food *ad libitum*: this allows cats to follow their frequent eating pattern but many of them appear to eat too much – hence the apparent increase in feline obesity. Risk factors may include the fact that pet food is very palatable and indoor cats, in particular, don't have much else to do. A further factor seems to be that cat owners may not understand what a normal bodyweight is for their cat, and tend to provide them with too much food, which the cats eat because it is so palatable.

Consequently, the American Association of Feline Practitioners recommends feeding cats in ways that stimulate their natural feeding behaviour e.g. supplying dry food through puzzle feeders, or hiding it around the house.

A further consideration, however, is that dry cat food in particular, and many tinned cat foods, are high in carbohydrates which are not a nutrient that cats in the wild eat. Therefore, endocrinologically, it may also be the nutrient content of commercial cat food and not simply its palatability or the cat's behaviour that predisposes pet cats to obesity.

Diseases of overfeeding in dogs and cats include diabetes mellitus, joint disease, liver disease, and heart disease.

Moving on to farm animals: in some countries, notably France, Hungary, and the US, ducks and geese are force-fed to make them ingest an excess of calories and so induce hepatic lipidosis. Their fatty livers are then used to make pate de foie gras (literally 'pate of fat liver') which is highly valued for its flavour.

Hepatic lipidosis is achieved by allowing the birds to increase their intake of food voluntarily, and then by force-feeding them: ducks, twice a day for 2 weeks; geese, three times a day for 3 weeks.

As a result the liver is 6-10 times the size that it would normally be, and liver function is impaired. Also, the birds have diarrhoea shortly after feeding. They pant more, and their abdomen is enlarged. However, research is lacking on whether the animals suffer because of this. It is likely that they feel abdominal discomfort because of the hypertrophied liver. Also, birds appear to try and avoid the handler when it is time to be force-fed.

We have already talked of how growing pigs and broiler birds have large appetites. By feeding them to appetite, they grow quickly but this results in health problems consequent on the strain placed on the heart (e.g. broilers are prone to cardiomyopathy and ascites) and skeleton (broilers and growing pigs are prone to various types of leg weakness and pain).

Slide 19:

Other examples of the problems caused by over-feeding animals are shown on this slide.

- Fatty liver in dairy cows occurs if their body condition score is too high, for example before calving (body condition >3 on a scale from 1 to 5) and fed too much concentrate. Affected cows are inappetent and unwell.
- Laminitis is inflammation of the hoof laminae. The condition is seen in horses and cattle if they eat large amounts of concentrate or rich grass that is high in protein. Laminitis is extremely painful and can allow rotation of the pedal bone and chronic lameness, even when the laminitis has subsided.
- Ruminal acidosis occurs when ruminants eat too much readily fermentable carbohydrate (e.g. when members of the public feed bread or cakes to deer, or when a farmer feeds too much concentrate to cows in the milking parlour. Affected animals are inappetent and depressed, and they may die from the metabolic consequences of the acidosis.
- Under-feeding is the opposite problem: this can affect animals' health status because it weakens the immune system and predisposes animals to infectious diseases, including parasitism.
- Neonates are particularly vulnerable to under-feeding, especially ungulates. Ungulate young need to suckle within the first few hours of birth in order to absorb maternal antibodies before the gut absorption mechanism for these large proteins is lost. If the animals do not receive colostrum early on they are prone to gastrointestinal and other infections, and have a high risk of dying from these infections.

The pig in the picture has deliberately been over-fed for a slaughter 'festival' in Taiwan.

Slide 20:

A further connection between food and disease concerns gastric ulceration in veal calves, which we will look at first, and horses.

- Ulcers of the abomasum are commonly found in veal calves on post-mortem examination. The prevalence of ulcers – which penetrate mucosa – and of erosions (non-penetrative) can range from 6–~76 per cent. The lesions are typically found on the pyloric region of the abomasum and in the fundic region.
- Eating roughage such as straw increases the incidence of pyloric ulceration, perhaps because straw abrades existing ulcers that have developed while the calves were fed only milk. In contrast, eating straw and solid foods reduces the occurrence of ulcers in the fundic region of the abomasum.

It seems that pyloric ulcers may be caused by the amount of milk drunk per feeding session – whether that is from buckets or from nipple-drinkers, and regardless of roughage intake.

In contrast, chronic stress may cause fundic ulcers and these may therefore be prevented by factors such as low stocking density, provision of roughage, and access to water.

Abomasal ulceration is difficult to diagnose, as many calves do not show symptoms, such as inappetence, or signs of abdominal pain. However, they may show oral stereotypies such as sham-chewing, tongue-rolling or bar-biting (pictured). While these behaviours may be, in part, a response to inadequate opportunities to forage, they may also be a response to ulcers because, by increasing saliva flow, they might reduce abomasal pH.

You can see from this that the relationship between diet and welfare in all senses (physical functioning, feelings and natural behaviour) is complex. Currently (2012), it remains unclear whether it is possible to feed veal calves in such a way as to ensure their welfare in all three areas while supplying the market for white meat. Some humane programmes promote 'rose veal', the pink colour of which results from (and is used to publicise) better and more natural diets.

In horses, crib-biting is a stereotypic behaviour in which the animal fixes his or her upper teeth on a fixed horizontal surface and makes swallowing movements. It is associated with gastric ulceration which may be seen in young weanlings as well as adults.

Being weaned onto concentrate food may increase the risk of developing crib-biting in horses: it is thought that crib-biting increases salivary flow and may be a response to increased gastric acidity caused by feeding concentrates.

Slide 21:

We now move away from the welfare effects of the relationship between food and disease to the connection between food and feelings. Food can be a source of fear and distress in various ways.

Predation: when prey species are hunted, they probably feel fear and distress, especially when they are cornered and are fighting for their lives. These negative emotions are very adaptive, but also very stressful. Predation is normally something that domesticated species are protected from.

However, the motivation to hunt prey may not be easily satisfied under captive conditions. For example, it can probably never be satisfied adequately in predators such as polar bears, who naturally roam over a wide territory.

Food can also cause distress if there is competition at feeding. Many species eat as a group: they are socially facilitated eaters, so when one animal eats, they all are motivated to eat. This includes cows, sheep, pigs and many fish species. When such animals are group-housed, there may not be enough feeding space for all animals to eat at once, or larger animals may keep smaller ones away. For the smaller animals, feeding may therefore be a source of fear and distress.

This may be made worse under conditions of quantitative dietary restriction: we noted earlier that this increases aggression in sows and in rats when they are group-housed.

A further consideration is that by selecting animals for fast growth rate, we may also have selected for those who are naturally more bold and competitive. Those who are less bold may avoid approaching the feeding area when food is delivered because they are frightened of the larger animals.

Slide 22:

An aspect of welfare related to the link between food and feelings of fear and distress is the connection between food and the behaviours that are important to the animal. We have already touched on this, in the cases of stereotypies shown by breeding stock of pigs and broilers on quantitative dietary restriction, and those shown by veal calves and horses in relation to feeding.

Other examples are found in dairy calves and piglets in association with early weaning.

Dairy calves are typically separated from their mother at birth or at least within four days. In many cases, the calves are then fed by bucket twice a day. They can drink these meals in a few minutes – much faster than if they were sucking milk through a teat or nipple. These calves typically show a lot of non-nutritive sucking – sucking on other calves or on parts of their enclosure, or sometimes drinking urine. This redirected sucking behaviour probably occurs because the rapid consumption of milk is not enough to satisfy the appetitive component of their feeding motivation.

However, when calves are allowed to drink milk *ad libitum* from containers with nipple attachments they show much less redirected sucking, while having good growth rates.

There are also negatives effects of early weaning on piglets.

Piglets are typically weaned at 21–28 days and group-housed in barren pens where there is no manipulable material. Often, some pigs in the group will bite the tails of others, which can produce infection, leading to spinal abscesses as well as causing stress in the bitten pig. Tail-biting may occur in pigs of different ages and it seems to result from a combination of factors, so it cannot be attributed to early weaning alone. However, providing piglets with manipulable material even while they are still with the sow helps to reduce the likelihood of an outbreak. This may be because the material helps piglets express appetitive feeding behaviour (rooting) so that they are less likely to direct this at each other.

Tail-biting has also been linked to nutritional deficiency. In one experiment (Beattie et al 2005), piglets' chewing behaviour towards ropes during the first 3 weeks after weaning was used as a surrogate measure of tail-biting. The researchers found that piglets who bit and chewed the ropes more had lower growth rates before and after weaning. The authors suggested that these lighter pigs received relatively less milk and were nutritionally deficient, or were chronically stressed in some way.

Lack of milk might cause pigs to have a strong drive to forage for food that would address the deficiency, and to direct their foraging at the tails of other pigs, which bleed and might satisfy the appetite for the missing nutrients.

Slide 23:

We have now covered many aspects of how food is related to animals' physical functioning, feelings/mental state and opportunities to perform important behaviours.

We started by looking at ways to balance the risk of obesity with the problems of dietary restriction in three groups of animals: laboratory rodents, the breeding stock of pigs, and broiler chickens.

We then expanded the lecture to consider how diet and methods of feeding can cause and be affected by other factors in different species:

- first we considered the effect of diseases on hunger and thirst
- then we considered the effect of food on animals' physical comfort (e.g. how adipose tissue is important for cushioning the body, and keeping the animal warm)
- we followed that with a brief look at how diet can cause diseases and how feeding can be associated with fear and distress and, finally, with problems associated with performance of species-typical feeding behaviours.

The lecture will end by looking at how to feed animals so as to enable them to perform more of both the appetitive and consummatory components of their feeding behaviour. We have touched on that in the discussion of nipple-feeders for dairy calves and providing manipulable material to young piglets. Those approaches are a form of environmental enrichment (EE), as we shall now see.

Slide 24:

Environmental enrichment is covered in detail in Module 15.

Nutritional EE is the alteration of the environment of captive animals in order to maximise the opportunity to show species-typical feeding behaviour.

As vets, you will be primarily concerned with the feeding of carnivores and herbivores.

Some important points about carnivores:

- carnivores eat to relieve hunger. Killing prey is potentially a risk as prey species will fight and can cause injury or escape altogether. So, carnivores invest and risk a lot of energy in feeding and it is important that the investment generates more energy than they expend
- as captive carnivores get hungry, they typically become restless
- if they are from species who chase and kill their food (e.g. mink) or who have to travel large distances to locate food sources (e.g. polar bears) they may develop locomotory stereotypies, often with elaborate patterns of pacing.

Some salient points about herbivores:

- most of our domestic animals are herbivores; they eat to prevent hunger

- herbivores may be loosely divided into 'browsers' and 'grazers' – browsers (e.g. goats) select particular patches or types of vegetation and use their teeth to cut it and draw it into the mouth; grazers (e.g. cattle) eat more uniformly and use their tongues to help pull the grass into the mouth
- many herbivores are herd animals for greater protection from predators
- stereotypies related to hunger and feeding are typically oral, such as tongue-rolling in cows and crib-biting in horses
- some species are omnivores (e.g. pigs); other species are insectivores and may eat foliage insects or air-borne insects; others are frugivores (eat fruit), granivores (eat seeds), piscivores (eat fish), etc.

Slide 25:

If you work in a zoo you will encounter the different types of feeders discussed above. When designing nutritional EE for them, you need to consider all aspects of their feeding behaviour.

This slide shows the points to consider for carnivores. Some of them can be applied to designing toys and feeding devices for pet cats.

Slide 26:

Herbivores and other non-meat eaters provide different challenges for the design of nutritional EE, as listed on this slide.

Slide 27:

This slide gives examples of ways in which you can provide nutritional EE.

- The first is by using puzzle-feeders – these are containers with holes in them. In order to extract food from the feeder, the animal has to manipulate it. Depending on the animal's natural feeding behaviour, the feeder may be a ball that the animal rolls or pushes (pigs, horses, cats), or it might allow the animal to insert a paw (cats).
- Feeding poles are used for large carnivores in zoos: the animal has to climb the pole to access meat or a carcass.
- Hiding food is a useful form of enrichment for most animals as it allows them to express the appetitive component of feeding motivation and, in many cases, to use their highly developed sense of smell (e.g. pigs, dogs, bears). Food can be hidden in different parts of the enclosure and the locations varied from day to day. Food can also be scattered through bedding. With both methods it is important to remove uneaten food so that it does not become rotten.

- Fresh food, e.g. fruits and vegetables for birds and rabbits, provides sensory enrichment for animals who are otherwise fed the same commercial diet day after day.
- Movement is an important aspect of feeding enrichment for carnivores. Many zoos have developed ways to feed their carnivores in as natural a way as possible. However, feeding live prey to captive carnivores should be avoided because of the suffering it can cause the prey (and feeding vertebrates as prey is illegal in some countries). The situation is not the same as it is in the wild, where the prey usually knows the territory and has some chance of escaping.
- We mentioned the importance of suckling behaviour earlier, in connection with dairy calves, and how nipple attachments enable animals to express this component of feeding behaviour.
- Variety provides sensory stimulation. Also, when the animal has access to different foods at the same time, he or she can exert some environmental control by choosing what to eat and when to eat it. For example, in a study of 12 competition horses, the horses showed a clear preference for having access to several different forages at once rather than only having access to one at a time. This was true even when the single forage was one that they had preferred over others when the feeds were all presented at the same time.

Slide 28:

To finish, we can say that acquiring food is an important activity for animals and how we feed them can give them pleasure or various negative feelings such as hunger and frustration.

By providing them with a readily accessible balanced diet we may assuage their hunger but we risk creating health problems related to over-feeding and other welfare problems such as frustration.

Dietary restriction may reduce some of those risks, but may not be enough to overcome the inherent problem of genetically-driven hunger in the breeding stock of fast-growing farm animals.

More generally, the content of the diet and the way it is delivered can promote or reduce different aspects of animal welfare, e.g. physical comfort, disease, negative emotions and the performance of important behaviours.

As veterinarians, it is important that you understand these ethological and logistical factors so that you can help your clients address the behavioural aspects of diet in animals in addition to the disease-related aspects.