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Predicting Feed Intake of Food-Producing Animals

Subcommittee on Feed Intake, Committee on Animal Nutrition, National Research Council

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Predicting Feed Intake of Food-Producing Animals

Subcommittee on Feed Intake
Committee on Animal Nutrition
Board on Agriculture
National Research Council

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NOTICE: The project that is the subject of this report was approved by the Governing Board of the National Research Council, whose members are drawn from the councils of the National Academy of Sciences, the National Academy of Engineering, and the Institute of Medicine. The members of the committee responsible for the report were chosen for their special competences and with regard for appropriate balance.

This report has been reviewed by a group other than the authors according to procedures approved by a Report Review Committee consisting of members of the National Academy of Sciences, the National Academy of Engineering, and the Institute of Medicine.

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Preface

In animal production enterprises, profits greatly depend on the ability to successfully maximize feed intake. It is essential, therefore, to understand the large number of physiological, environmental, and management factors that influence feed intake. Although there is still much to learn, scientists and producers have identified many of these factors through research and experience. Data are also available to quantify them.

The twofold purpose of this report is to discuss control mechanisms of feed intake and to quantify intake for each of the animals commonly used for food and fiber in the United States. For each species, a separate chapter provides equations and adjustment factors that can be used to predict dry matter intake, tests these equations and factors using independent data, and identifies areas that need further research.

The widespread use of microcomputers makes diet evaluation and performance projections feasible. Our goal was to assemble the best information available in a usable form to allow accurate predictions of intake under widely varying conditions. The subcommittee chose to present specific applications rather than more complete models because of the rapid evolution of approaches to computerization. However, factors may be easily adjusted to suit the user's particular needs. We hope that a better understanding of factors involved in feed intake will lead to more efficient formulation of animal diets.

The Subcommittee on Feed Intake was appointed in 1982 under the auspices of the Board on Agriculture's Committee on Animal Nutrition (CAN) to develop recommendations for predicting intake of animals. The report includes chapters on all major food-producing animals. The following individuals were responsible for respective sections of the report: Clifton A. Baile, Introduction: Feed Intake Control Mechanisms; Gary L. Rumsey, Fish; Richard Ewan, Swine; Park W. Waldroup, Poultry; H. Russell Conrad, Dairy Cattle; and Danny G. Fox, Beef Cattle and Sheep. Ling-Jung Koong reviewed prediction equations in the species chapters and provided advice on validation procedures.

This report was reviewed by the Committee on Animal Nutrition; the Board on Agriculture; and 13 outside reviewers—David H. Baker, Lane O. Ely, Richard D. Goodrich, Wayne J. Kuenzel, Leo S. Jensen, Santosh P. Lall, David R. Mertens, Donald Polin, Hugh A. Poston, Rodney L. Preston, Nathan E. Smith, Richard G. Shields, and T. S. Stahly. The subcommittee is grateful for the efforts of these individuals and thanks Deena H. Krestel-Rickert for her assistance in preparing the introductory chapter. We especially acknowledge the contributions of Selma P. Baron, who served as staff officer during the early preparation of this report.

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Introduction: Feed Intake Control Mechanisms

INTRODUCTION

The control of feed intake and regulation of energy balance are influenced by a number of factors. A regulator of body energy content is apparently interfaced with a controller of feed intake that maintains a balance of energy input and output under normal conditions. However, under certain circumstances, the system can be overridden and result in excessive weight gain or loss (Baile and Forbes, 1974). Subsequently, either condition could lead to metabolic disturbances and inefficient production.

Feeding behavior can be influenced by several external factors such as environmental conditions, sensory cues, and nutrients in the diet. The internal milieu of an animal, including gastrointestinal factors, hormones, and metabolites, also plays a role in feeding behavior.

The primary site responsible for the integrated control of feed intake and energy balance is the central nervous system (CNS), although the specific mechanisms involved are not well understood. Peptides found in the CNS have been shown to have a direct effect on the control of metabolism, feed intake, and reproductive behaviors. For instance, the onset of feeding may be influenced by opioid peptides, and termination of feeding may involve cholecystokinin. A number of CNS and most likely peripheral receptor systems exist that provide information about the animal's metabolic state. A coordinated feeding behavior is established via these receptor systems and CNS centers.

Factors involved in the control of feed intake and energy balance are reviewed in this chapter. A comparison is made between and within species regarding the mechanisms that influence energy balance. The controlling factors considered include those associated with the gut and brain of the animal.

OVERVIEW OF CONTROL SYSTEMS

Several metabolic and sensory factors are known to affect meal size and frequency. While meal size can vary greatly, the total quantity eaten each day, for example, must be controlled to maintain energy balance. The signals of satiety that control individual meal size must have shorter time constants than the signals that regulate long-term energy balance. Feeding behavior is also influenced by certain hormones and metabolites as well as gastrointestinal factors. Understanding the mechanisms involved in signaling the controller of feed intake may lead to improved methods of animal production.

Digestive Tract

In ruminants it has been hypothesized that the amount of forage eaten at a meal might be limited by the capacity of the rumen (Campling, 1970). When cattle were offered feed for about 6 h/day, the weight of the digesta of the rumen compared to that at the beginning of feeding increased by 48 percent and dry matter increased by 96 percent. Regardless of the range of feeds or types of cattle tested, these increases were consistent, supporting the idea that cattle eat until a certain proportional change of ruminal distension is achieved. Recent evidence suggests that the distension may be detected by tension receptors with varying neural adaptation times that are thought to exist in the ruminant stomach. These receptors have not been histologically identified as yet. Grovum (1979) has reported that sheep reduce feed intake in response to distension of the reticulum, and thus, the sheep's reticulum may possess stretch receptors that are sensitive to distension of the gut after a meal.

Digestibility of the foods that ruminants consume can easily be related to the kinetics of digestion and its passage from the rumen (Waldo, 1969; Mertens, 1973). Forage intake is related to fiber digestion because it is limited by the rate of disappearance of material from the digestive tract (Conrad et al., 1964; Thorter and Minson, 1972; Mertens, 1973). Mertens and Ely (1979, 1982) have proposed a model of fiber disappearance from the digestive tract in ruminants. They have suggested that the ruminant's digestive process is divided into rates of digestion, digestion lag, and potentially digestible fraction. The retention time in the entire digestive tract is influenced by level of intake, physical characteristics of the diet, and rumination time. Specifically, their model suggests that maximum intake of digestible dry matter is affected more by the proportion of indigestible fiber and rate of passage than by the rate of fiber digestion.

In general, increasing the level of feeding to twice maintenance results in a 1 to 2 percent reduction in dry matter digestibility of feed for the ruminant. This reduction can vary with the quality and grind of the feed. In the pig, digestibility decreases with increases in level of feeding but to a lesser extent than in ruminants (McDonald et al., 1973).

Utilization of end products of digestion also differs widely between ruminants and monogastric animals. Non-ruminant herbivores, e.g., equines, absorb many products of digestion in the small intestine and utilize them as a source of energy as efficiently as carnivores and omnivores (Roberts, 1975; Hansen et al., 1981). Microbial fermentation of ingesta in the equine cecum and large colon can provide as much as 60 percent of the total digestible energy available from the diet. This energy source is in the form of short-chain volatile fatty acids (VFAs). VFAs are the primary energy source in ruminants, but are provided by fermentation in the rumen, which is anterior to the small intestine. During and after feeding the VFA concentrations in the rumen fluid and blood increase (Chase et al., 1977); these changes are most obvious in sheep and cattle adapted to limited feed access. During limited feed access smaller increases in VFA concentrations occur during smaller spontaneous meals. Large differences in VFA concentrations can exist in various parts of the rumen for several hours after large meals due to slow mixing within the rumen.

In ruminants acetate and propionate appear to play a role in the control of meal size. Intraruminal injections of either metabolite depress feed intake in cattle, sheep, and goats (Baile and Mayer, 1970; Baile and Forbes, 1974). There are similarities that exist between the effects of acetate and propionate in that they can both depress feed intake, but different receptors are thought to exist for each in the ruminal area. It has been demonstrated that there are chemoreceptors present in the wall of the rumen that are sensitive to changes in pH but not specifically to acetate (Harding and Leek, 1972). When infusions were made into the ruminal vein, propionate was most effective in depressing intake, suggesting that propionate receptors are present in the wall of that vein. Anil and Forbes' (1980a) work further substantiated that propionate depresses feed intake more than acetate or butyrate. Sheep receiving a 3-h infusion of sodium propionate into the portal vein ceased eating 30 min after the onset of the infusion until the end of infusion. If the hepatic plexus was denervated, feeding continued during portal propionate infusion, suggesting that the liver is a major site for mediating the effect of this VFA on feeding.

The question has been raised regarding the effects of propionate infusions via the portal vein on blood composition. Results may be hampered by the uncertainty of whether induced blood changes remain within the normal physiological levels. De Jong (1981) showed that the change in VFA levels occurred in animals that were fed once or twice daily. This scheduled feeding regime is associated with large quantities of food eaten in a short period of time and is different from those meals eaten by animals on a flee-feeding schedule. De Jong (1981) and De Jong and coworkers (1981) infused isotonic or hyper-tonic solutions of sodium salts of VFAs (acetate, propionate, *n*-butyrate, isobutyrate, or lactate) at a constant rate for 4 h via portal vein catheters into free-feeding adult goats. The results did not support the contention that VFAs have a function in the control of feed intake, and it was concluded that a role of the VFAs in the control of feed intake did not involve blood concentration changes.

Ruminant feeding behavior can also be influenced by changes in osmolarity of body fluids. Increases in rumen fluid osmolarity from about 250 to 350 mOsM during rapid eating of large meals can produce hypertonicity of body fluids and result in dramatic circulatory and renal changes. For instance, sheep can experience a rise in systolic blood pressure and a reduction in plasma volume within 15 min of the initiation of rapid feeding (Blair-West and Brook, 1969). This is probably due to the transfer of Na^+ and water from body fluid to rumen fluid. These mechanisms may cause ruminants as well as other mammals not to eat if they are severely dehydrated (Utley et al., 1970). Thus, water consumption and changes in body fluids play a role in the control of feed intake. However, in animals not deprived of water or in which feed consumption is slow or feed is taken in small meals, changes in the rumen or body fluid tonicity are unlikely to limit feed intake.

Metabolites

Glucose has long been considered to be an integral component of the feeding control system in monogastric animals. It has been shown that dramatically reduced rates of glucose utilization associated with administration of glucose analogs or insulin-induced hypoglycemia produce feeding and hunger, whereas increased glucose utilization rates as well as hyperglycemia do not appear to affect feeding (Baile and Mayer, 1969). In the ruminant, blood glucose concentration, arteriovenous differences in glucose concentration, and glucose utilization rates generally decrease rather than increase with feeding (Baile and Forbes, 1974). Thus, there is less evidence that glucose utilization or concentration plays a significant role in controlling feeding in the ruminant (Baile and Della-Fera, 1981); in fact, there has been substantial evidence that supports the contrary.

Meal size was depressed in the pig by duodenal injections of isosmotic solutions of glucose and NaCl via implanted catheters (Houpt et al., 1983a,b). Injections were made after the onset of alternate meals throughout the day. Injections of 5 ml/kg of 5, 20, and 40 percent glucose and 0.9, 3.25, and 6.5 percent NaCl equally depressed the size of an ongoing meal proportionately with respect to their hypertonicity. Neither intermeal interval nor rate of eating changed to account for the reduction of meal size; only meal duration decreased. Such results are indicative of a possible duodenal osmoreceptive system which may be involved in controlling the size of a meal.

In sheep, feeding of concentrate (feed that is more calorically dense than average) can be reduced by high physiological duodenal concentrations of lactate and lactic acid. Receptors in the sheep's duodenum are particularly sensitive to these metabolites (Bueno, 1975). This reduction in feeding may be a result of depressed stomach motility or a feedback effect to the CNS from the duodenal receptors.

Amino acids, e.g., lysine and glycine, may play a role in the control of feeding (Baile and Martin, 1971). In sheep, plasma amino acid levels decline after a single daily feeding but increase a few hours later, reaching their maximum at about 24 h postmeal. Meal size of ruminants is probably unrelated to the absorption of amino acids since they are supplied primarily by the small intestine several hours after ingestion. With respect to amino acid imbalances or protein deficiencies, the suckling (preruminant) lamb will decrease feed intake by one-half in response to a diet low in total protein or void of either isoleucine or threonine (Rogers and Egan, 1975). Therefore, changes in plasma amino acid levels do not appear to directly affect the feed intake of ruminants fed a balanced diet.

The increase in free fatty acids (FFAs) associated with starvation has been suggested to act as a signal to induce feeding, despite the fact that FFAs increase not only with energy depot mobilization but also with feeding in animals adapted to a daily feeding schedule (Chase et al., 1977). Feed intake in sheep was depressed by intraduodenal injections of long-chain fatty acids or fats, but it remains unclear if depression in ruminoreticulum movements or changes in blood fatty acid composition was the cause (Titchen et al., 1966). Thus, there is insufficient evidence as to whether FFAs are a cause rather than an effect of changes in feeding.

Hormones

Hormones considered for their possible role in controlling feed intake include two of pancreatic origin, glucagon and insulin. Experimental work with glucagon was initiated in 1955 by Stunkard et al., in which intravenous infusions of glucagon brought about the sense of satiety in humans. This work has been extended to other species (Penick and Hinkle, 1961; VanderWeele et al., 1979). Glycogenolysis is the major metabolic action of glucagon in the liver and was considered as the mechanism of action for satiety (Geary et al., 1981). But when glucagon was injected intraperitoneally and the expected glycogenolysis occurred, it had no effect on sham feeding (Geary and Smith, 1982a). Langhans et al. (1982a) demonstrated that glucagon doses required to reduce meal size produced changes in hepatic metabolism that are also present at the end of normal meals, e.g., reduced liver glycogen content; but in several instances it has been shown that the hyperglycemic response to glucagon is not sufficient to cause the satiety response (Geary and Smith, 1982b). Some of the most convincing evidence that supports glucagon's role as a satiety factor is provided by Langhans et al. (1982b), who showed that glucagon antibody injections in rats cause increased feeding. Intraperitoneal injections of rabbit antibodies against purified bovine pancreatic glucagon or serum from nonimmunized rabbits were administered at the beginning of the first meal of a dark phase and after a 12-h fast. Feeding increased markedly (63 percent) in these rats versus that in controls, as did meal duration (74 percent). It was concluded that the glucagon released during feeding was sequestered by the antibody and thus removed a proposed essential component for satiety.

McLaughlin et al. (1984) have demonstrated that female Zucker obese and lean rats decreased daily food intake when immunized against pancreatic glucagon (conjugated to bovine serum albumin). Over a 16-week period, not only did food intake decrease 5.0 percent but weight gains decreased 9.4 percent as well. These results appear contradictory to the hypothesized outcome (Langhans et al., 1982a; McLaughlin et al., 1983a) of increased food intake brought on by immunization against glucagon. However, the observed decreases may well be a consequence of an overcompensatory in crease in total (free and antibody-bound) serum glucagon concentrations.

Over the last several decades the hypotheses regarding insulin's involvement in the control of food intake have varied. While hypoinsulinemia does not result in anorexia, feeding can be induced by injections of insulin but only after severe hypoglycemia occurs; yet insulin can also be associated with overeating (Brandes, 1977). Hyperphagia and hyperinsulinemia, but not hypoglycemia, often occur with the development of obesity (Jeanrenaud, 1979). The causes for such associations are not well understood, but insulin resistance is a common factor. Acute and persistent changes in plasma insulin concentration may have opposing effects on feeding. Porte and Woods (1981) proposed that insulin may be a body adiposity signal. Factors that influence the control of food intake may be classified into two categories: (1) factors that cause feeding behavior to change independent of body stores and (2) factors that are sensitive to the size of the adipose mass. The second category involves insulin as the hormone that. signals meal feeding to maintain energy balance. This proposal is based on the observations that the plasma insulin concentration increases with the severity of adiposity. Since levels of insulin fluctuate frequently within a 24-h period, it is likely that some means is essential for obtaining an integrated response with a relatively slow time constant. Porte and Woods (1981) hypothesized that insulin in the cerebrospinal fluid (CSF) may possess such a means. Concentrations of CSF insulin change with plasma concentrations but at a much slower rate, with a half-life of hours as opposed to minutes.

Further evidence in support of this hypothesis is provided by continuous lateral ventricular injections of insulin in the baboon over a 14-day period, resulting in a reduction in food intake and body weight (Woods et al., 1979). Similar glucagon injections had no effect, which suggests that the response was caused by a specific peptide. However, many studies have demonstrated that insulin and glucagon have influential roles in controlling feeding behavior and in the regulation of energy balance. Still, much remains to be done toward proving the association of CSF insulin and energy balance regulation and glucagon's role in feeding before these two pancreatic hormones can be considered as satiety signals.

Insulin's effectiveness as a satiety hormone has also been investigated in swine (Anika et al., 1980). Following a 4-h fast, doses of insulin (0.05, 0.13, and 0.25 U/kg) delivered via intrajugular catheters produced a depression of feed intake compared to that in controls. Other doses (0.03, 0.5, and 1.0 U/kg) of insulin did not produce similar effects during the first 10-min feeding period. However, significant depression of feeding did occur in the second 10-min period with the higher doses (0.13, 0.25, and 0.5 U/kg). Anika et al. (1980) suggest that prandially released insulin, whether released by the action of cholecystokinin or glucose absorption, for example, may be influential in bringing a meal to an end.

An interrelationship between insulin and growth hormone (GH) during lipogenesis has been noted by Graham (1967). A high insulin:GH plasma ratio is required for lipogenesis, and this ratio occurs in sheep after meals scheduled at 3-h intervals, whereas lipolysis is stimulated by a low insulin:GH ratio. A decline in the insulin:GH ratio might be expected to occur at the start of a meal if a shortage of absorbed energy triggers lipolysis and feeding. Driver has observed peaks of GH every 2 to 4 h in sheep with free access to food, and he noted that spontaneous feeding did not occur when the GH concentration was high (Driver and Forbes, 1978; Driver et al., 1979). Forbes (1980a,b) suggested that elevated plasma GH levels do not directly inhibit feeding but that this provides evidence for a link between the initiation of feeding and a deficit of energy-yielding metabolites.

Brain

The hypothalamus is directly and indirectly involved in the control of systems and variations of body energy content. The center controlling energy balance in the brain is classically the ventromedial nuclear region of the hypothalamus (VMH). Stimulation of this satiety center inhibits feeding (Hetherington and Ranson, 1939). If complete or partial lesions are made in the entire area, they usually produce an immediate hyperphagia and weight gain that eventually stabilizes at a higher set point and the hyperphagia subsides. Controversy exists over whether VMH lesions induce hyperphagia since some studies have shown that damage to the proximal catecholaminergic pathways can influence feeding. However, these pathways do not synapse in the VMH (Ahlskog and Hoebel, 1973; Gold, 1973).

Much of the early work on the role that the brain plays in controlling feed intake was conducted on rats, but other species, i.e., ruminant and nonruminant domestic animals, have been considered as well. Baile et al. (1968a,b) demonstrated that goats with bilateral lesions of the lateral hypothalamic area became temporarily aphagic and adipsic, and lesions of the ventromedial area produced hyperphagia and substantial weight gain. Aphagia and adipsia can also be induced by lesions of the lateral area of the hypothalamus in swine (Khalaf and Robinson, 1972) and sheep (Tarttelin and Bell, 1968).

In the chicken the hypothalamus is also the site of many food-regulatory effector functions. Several physi ological changes have been noted to occur in the chicken when electrolytic lesions are made, but only those relevant to feed intake will be considered here. Some hypo-thalamic lesions produce aphagia (Feldman et al., 1957), and hyperphagia accompanies functional castration, but no hyperphagia has occurred in permanently castrated males and females (Snapir et al., 1969). Properly placed lesions normally produced increases in body weight as a result of the production and accumulation of excess fat. However, occasionally no effect results. A typical hypothalamic obesity can be demonstrated in the chicken with basomedial hypothalamic (BMH) lesions (Robinzon et al., 1977a). Placement of bilateral septal lesions by intracranial injection of 6-hydroxydopamine in geese produced a significant increase in feed intake (Snapir et al., 1976). In contrast to the hypothalamic obesity brought about by BMH lesions, septally lesioned geese and cocks did not develop obesity but were hyperphagic (Snapir et al., 1976; Robinzon et al., 1978). These results with geese are similar to those obtained from bulbectomized chickens, in which a marked increase in feed intake occurred without obesity (Robinzon et al., 1977b).

Thus, lesions of the hypothalamus produce a number of effects related to the control of feed intake in both ruminant and monogastric animals. However, there are probably differences in the feedback and receptor systems involved in energy balance for each type.

The route via which information travels from the sensor of energy balance to the hypothalamus is not clear, although the bloodstream has been suggested as a possible pathway for such communication. Hervey (1959) noted metabolic adaptations that occurred in parabiotic pairs of rats. When the VMH of one partner of a pair was lesioned, it became obese while the other partner became thin and died apparently from inanition. It has been suggested that the nonlesioned hypothalamus of the one partner responded to the total positive energy balance of both rats by reducing its food intake. Subsequently, only its own body weight was affected and not that of the obese rat. More recently, parabiotic rats have been used to demonstrate the existence of endogenous factors that separately control feed intake and metabolism of body fat. Kasser et al. (1984) have shown that the hypothalamic tissue pentose phosphate pathway can be uniquely altered, supporting the concept of an eminent role for CNS metabolism in controlling feed intake. It is clear that the hypothalamus plays a primary and critical function in the regulation of energy balance in animals.

Other Factors

Factors other than those previously mentioned can affect feeding behavior. Sensory cues of olfaction and taste can influence the selection and consumption of various foods for most species. Ruminant animals are capable of utilizing a variety of waste products as feed-stuffs. However, many of these products are unpalatable and not utilized to their fullest extent. Olfactory cues can influence whether or not a meal will be initiated, and taste may affect the length of that meal. It appears that species variability does exist with regard to taste preferences. However, most species exhibit a preference for sweet tastes (Hellenkant, 1978). Although palatable flavors can increase feed intake in many species (Baldwin, 1978), only a few flavors have been tested systematically (Zivkovic, 1978; McLaughlin et al., 1983a).

Ammonium ions, i.e., urea, whether injected or used as a diet supplement, are also effective in controlling feeding. Baile (cited in Conrad et al., 1977) demonstrated that ammonium infusions into the rumen failed to reduce rumen motility until lethal levels had been added. Conrad et al. (1977) found that an intraruminal injection of an ammonium load in goats during spontaneous meals reduced meal length, rate of eating, and meal frequency. They also reported that when urea was added to the diets of cows, the first meal length, as well as meal size, was decreased, but total feed intake was unaffected since the number of spontaneous meals increased. Thus, those physiological factors that limit meal length with urea in the rations are undefined, yet they are important considerations in the successful feeding of cows in situations where eating time is limited.

Other factors that can affect feed intake are temperature and environmental conditions. Growth or lactation in an animal can be reduced by heat stress in some species, but the critical temperatures at which effects become noticeable vary within and between species. Feeding can be inhibited by extreme heat loads, but it has been postulated that this may be a stress-related response as opposed to a normal satiety signal. However, most species do have a uniform milk production rate and feed efficiency over a relatively wide range of conditions.

Sex hormones are also influential in determining amounts of feed eaten by animals. When weight gain is induced in rats by progesterone, the increase in feed intake is more variable than the weight gain. In fact, when feed is restricted to the control intake, progesterone treatment produces two-thirds of the additional energy storage that occurs in free-fed rats (Hervey and Hervey, 1967), thus indicating a decreased energy expenditure.

Estrogen has been suggested as a factor that can affect feed intake by acting on an area of known sensitivity in the anterior hypothalamus (AH) which sends projections to the VMH (Kennedy and Mitra, 1963;

Kennedy, 1964). More recently, Wade and Zucker (1970a,b) have demonstrated that estradiol can act directly on the VMH. The result was a depression of feed intake, which was apparently an estrogen-induced action; however, this depression was not observed in weanling rats under 40 days of age unless they were hypophysectomized.

They concluded that before puberty pituitary hormones blocked the VMH restraint on intake. There must be other sites of action involved in estrogen's effects on feed intake since estrogens are capable of stimulating eating in rats that have access to exercise wheels. This occurs indirectly by stimulating locomotive activity, hence increasing energy expenditure, and lesions of the AH block this locomotor action of estrogen. High levels of estrogens are generally considered to inhibit growth which in turn can depress feed intake. Tarttelin (1968) has also reported depressed feed intake coinciding with estrus in the ewe. Growth and intake do not appear to be affected by estrogens in the prepubertal rat, but after puberty estrogens do have an effect on intake (Wade and Zucker, 1970a,b).

Diethylstilbestrol (DES) has been used as a feed additive or as an ear implant for stimulating weight gains and improving feed efficiency of growing and finishing ruminants (Riggs, 1958; National Research Council, 1963). It has also been reported by Trenkle (1969) that estrogenic compounds, e.g., DES, produce only a slight increase in feed intake.

Other steriods, e.g., dehydroepiandrosterone (DHEA), a 17-ketosteroid, can produce a decrease in weight gain without affecting feed intake in lean mice and yellow obese mice that have hypertrophic adipose tissue (Yen et al., 1977; Cleary et al., 1982). Not only was body weight reduced but the feed efficiency ratio, fat cell number, and size of the fat cell were significantly decreased (Cleary et al., 1984).

In the Leghorn cock testosterone propionate (TP) is effective in inducing hypophagia and, in turn, reducing carcass fat content, while DES increased adiposity markedly through hyperphagia. Injections of the combined steroids (TP and DES) produced only moderate obesity (Snapir et al., 1983). The results suggest that TP may decrease feed intake and lipogenesis, whereas DES has the opposite effect.

REGULATORY PEPTIDES

Other hormones are involved in the regulation of energy balance and control of feeding behavior, including peptides of the gastrointestinal (GI) tract and brain. For years knowledge of GI hormones was limited to the existence of three or four, but now many GI peptides are known to exist. Many of their actions remain undefined, however. While advances have been made in the area of regulatory peptides within the last decade, much remains to be discovered with respect to synthesis, release, and actions of the various forms of the peptides. One GI hormone for which there is evidence for a role in controlling feed intake is cholecystokinin (CCK).

Cholecystokinin

Gibbs et al. (1973) showed that CCK is capable of inhibiting feed intake. Studies have revealed that sham-fed fistulated rats decreased feed intake following intraperitoneal or intravenous (IV) injections of CCK, and the observed percentage of inhibition of feed intake was dose dependent (Lorenz et al., 1979).

The specificity of CCK has been clearly demonstrated by comparing the effects of closely related peptides. A sulfate group present on the seventh amino acid, tyro-sine, can influence the actions and receptor-binding affinities of CCK-active peptides (Steigerwalt and Williams, 1981) and is necessary for the satiety effect (Ondetti et al., 1970). The desulfated CCK is far less active than the sulfated form; for example, Lorenz et al. (1979) reported the potency of desulfated CCK-8 to be 10 times less than that of the sulfated form in inhibiting feeding.

Over the last decade the effects of CCK on the feeding behavior of food-producing animals have been studied. Intraportal injections of CCK in pigs proved to be more effective in inhibiting intake than intrajugular injections, whereas intraperitoneal injections were significantly less effective than injection at either intravenous site (Anika et al., 1981). In comparison, peripherally administered CCK produced very little or no effect on feed intake in sheep (Baile and Grovum, 1974; Anil and Forbes, 1980b). However, if a small dose of an impure CCK-33 preparation was injected intrajugularly over a 296-min period, a decrease of 40 percent in intake occurred within the first 10 min of injection. This decrease did not persist over subsequent time periods, despite the continuation of the injection (Grovum, 1981). In chickens intravenous injections of CCK-8 or caerulein decreased feeding within the first 10 min of injection and then normal feed intake resumed (Savory and Gentle, 1980). Feeding was also shown to decrease after administration of a CCK-33 preparation in a different test system (Snapir and Glick, 1978).

There are variations in the effects of CCK between species. Effects of CCK may vary due to interspecies rate of digestion. In chickens, for instance, feed first passes through the crop and gizzard, delaying the arrival of the ingesta to the intestines and, in turn, delaying the release and effect of intestinal CCK. Savory and

Gentle (1980) proposed that meals that were greater than 6 min in length could be influenced by CCK released from the duodenum as a result of the newly ingested food reaching that part of the intestinal tract. In sheep there is also a delay of intestinal digestion since food is held in the rumen, subjected to microbial digestion, and then slowly passed to the intestines. Therefore, GI CCK may not work as a satiety agent in sheep and chickens by the same route as in other animals, such as pigs. These characteristics should be considered when evaluating the effectiveness of gut hormones on feeding behavior.

Despite the finding that exogenous administration of CCK results in decreased feed intake in several species, little conclusive evidence exists that supports the fact that CCK is essential for satiety to occur. Recently, McLaughlin et al. (1985) used antibodies (AB) to CCK to sequester endogenous CCK to determine the effect on feed intake. Zucker lean rats were autoimmunized using a conjugated CCK-8. Both average daily feed intake and weight gain increased in immunized rats versus controls. Sequestering of CCK released during a meal increased meal size, and in those animals that developed significant endogenous CCK-AB titers daily feed intake and weight gain increased. These data provide strong evidence that CCK may play a role in satiety.

Several other experimental approaches have been used to demonstrate that endogenous CCK might mediate intestinal satiety. Some amino acids, in particular *l*-phenylalanine, in the lumen of the small intestine causes CCK to be released. If infused intragastrically in monkeys, *l*-phenylalanine decreased feed intake, whereas *d*-phenylalanine was ineffective (Gibbs et al., 1976). Evidence exists for a negative feedback control of CCK release by trypsin in the lumen (Brande and Morgan, 1981). Oral administration of a trypsin inhibitor causes a decrease in trypsin activity and decreases CCK content in the intestinal mucosa (implying CCK release). This inhibitor also increases the secretion of pancreatic enzymes, a known effect of CCK. Brande and Morgan (1981) suggest that by changing the level of trypsin activity in the gut it is possible to alter the amount of CCK released. Other work indicates that trypsin inhibitors decrease feed intake in rats and that trypsin supplements can increase intake (McLaughlin et al., 1983b,c).

Numerous studies have demonstrated the presence of CCK peptides in the brain of both mammalian and non-mammalian species. At least five forms of CCK are known to exist: a component larger than CCK-39, a component similar to CCK-39, CCK-12, CCK-8, and CCK-4. Of these forms CCK-8 is the predominant form in the brain (Rehfeld, 1978; Rehfeld et. al., 1979; Goitermann et al., 1980). There appears to be a specificity of regional distribution of CCK peptides and receptors in the brain. The highest concentration of CCK and its receptors occurs in the cortex; however, significant quantities of CCK-8 have been located in the hippocampus, periaqueductal gray, and dorsomedial hypothalamus as well (Rehfeld, 1978; Saito et al., 1980; Beinfeld et al., 1981).

Evidence that supports the role of brain CCK peptides in satiety has been obtained from experiments in which lateral ventricular (LV) injections of CCK were made in sheep (Della-Fera and Baile, 1979; Della-Fera et al., 1981) and pigs (Parrott and Baldwin, 1981). Significant decreases in feeding occurred when fasted sheep were administered as little as 0.01 pmol of CCK-8/min. Larger doses of 2.5 pmol of CCK-8/min or greater suppressed all feed intake during 3-h injection periods (Della-Fera and Baile, 1979). With respect to fasted pigs, feed intake also decreased in a dose-dependent manner. In both species CCK-8 affected only feed intake without affecting water intake or body temperature (Della-Fera and Baile, 1980a; Parrott and Baldwin, 1981). Amounts of CCK-8 required to induce this response were similar between species.

Experiments in which CCK antiserum was injected into the LV of sheep provide the strongest evidence for CCK's involvement in satiety (Della-Fera et al., 1981). Significant increases in feed intake occurred during injection of antiserum versus injection of normal control serum. The pattern of increased feed intake may have been related to an inhibition of satiety as opposed to the stimulation of hunger, since typical postmeal intervals did not occur during injection of CCK antiserum but did occur with the control. The early onset of increased feeding in association with injections of CCK antiserum indicated that CCK antibody may have been effective by sequestering CCK in the CSF. CCK may have been released into the CSF prior to interaction with the receptors that mediate the satiety effect; thus, it is possible that CCK is transported via CSF to its sites of uptake or action (Della-Fera et al., 1981).

In experiments with chickens, in which 4-week-old broilers were injected intracerebroventricularly with doses of 100 and 150 ng, CCK-8 reduced feed intake over a period of 60 and 105 min, respectively. Feed intake was reduced by 87 percent for the first 15 min postinjection of 150 ng of CCK-8 (Denbow and Myers, 1982). This decrease was nearly fourfold greater with less than one-third the amount injected intravenously by Savory and Gentle (1980). In the latter studies subjects were 12- to 17-week-old hens and thus larger in body mass. When injected with 40 times the amount of CCK-8 used by Denbow and Myers (1982), feed intake was only reduced by approximately 45 percent.

The mechanism of action of CCK's central effect on feeding behavior is not yet clearly defined. The problem is complex in that centrally administered CCK can produce changes in GI function (Della-Fera and Baile, 1980a,b; Bueno et al., 1983) and secretion of specific hormones (Della-Fera and Baile, 1981). The possibility exists that the effects of brain CCK may be mediated through the release of other brain peptides such as calcitonin (Care et al., 1971) or neurotransmitters such as norepinephrine (McCaleb and Myers, 1980). Clearly, much more information is required to propose a unifying hypothesis for these actions of CCK.

Opioid Peptides

Recently, evidence has been generated that indicates a role for certain brain peptides such as neurohormones or neurotransmitters in hunger and satiety. Opioid peptides have been implicated in several bodily functions and processes (Terenius, 1978; Margules et al., 1979; Amir et al., 1980), including feeding and ingestive behavior (Morley, 1980). An opiate receptor system has been suggested as a component in initiation of hunger in the ruminant (Baile et al., 1981).

A broad spectrum of opiate agonists and antagonists have been tested to determine the mechanisms involved and the class(es) of opiate receptors responsible for opiate-induced feeding. Feeding can be stimulated in sheep receiving injections ICV of opioid peptides; e.g., an enkephalin analog can stimulate satiated sheep to eat (Baile et al., 1981). Opiate antagonists, such as naloxone, can suppress feeding in sheep (Baile et al., 1981; Bueno et al., 1983), guinea pigs (Schulz et al., 1980), rabbits (Sanger and McCarthy, 1981), and mice (Holtzman, 1974). Naloxone-injected IV in combination with an LV injection of enkephalamide eliminates the feeding responses of enkephalamide (Bueno et al., 1983).

In yet another series of experiments, IV injections of a similar enkephalin analog (Tyr-D-Ala-Gly-Phe-N[CH^3]-L-PheNH_2-HOAc) stimulated feeding in satiated sheep (approximately 50-kg body weight). An approximate 14-fold increase of peptide was required for this response versus the amount of analog used in the LV study (12.25 versus 0.92 mg) (Baile et al., 1981). The findings from these LV studies are indicative of the fact that CNS is a likely site of action for opioid peptides, but it remains to be shown where the IV-injected peptides act.

Another opioid peptide associated with the hunger component of feed intake is -endorphin. Increased plasma -endorphin concentrations have been shown to be related to hunger (McLaughlin and Baile, 1985). They postulated that if rats were immunized against -endorphin, antibodies would sequester -endorphin and produce a decrease in feed intake and body weight. In fact, rats autoimmunized against -endorphin increased feed intake and body weight. It is not clear if these responses are due to a decreased free concentration or an increased total concentration of plasma -endorphin. Increased production of other proopicorticotropin cleavage products, e.g., adrenocorticotropic hormone, in these rats may contribute to the observed increases in feed intake, body weight, and pituitary size.

On the basis of various studies showing that different opiate agonists bind different classes of receptors with varying affinities, some tentative conclusions concerning specific receptor systems involved in feeding can be drawn. It appears that kappa- and mu-opiate receptors may be particularly important in the hyperphagic response since opiates that are relatively specific for either of these types of receptors are highly effective in inducing feeding (Larrson and Rehfeld, 1979; Yim et al., 1980; Morley and Levine, 1981).

In an effort to test the differential roles that opiate receptor subtypes play in feed intake, Della-Fera et al. (1983) tested D-alanine (2D-Ala) dynorphin (dyn)-17 and dyn-13, and dyn-17. Feed intake was increased during a 60-min LV injection in sheep. Dyn- had no effect, whereas (2D-Ala 5_{Leu}) enkephalin (DADL) decreased feed intake. Della-Fera et al. (1983) suggested that since dyn-A and DADL act on receptors other than kappa and delta, that exclusivity may not exist for their action at the receptor level.

The specific sites of opiate receptors involved in the feeding responses and the mechanism of opiate action responsible for eliciting feeding remain unknown. Some evidence does exist, however, for an interaction between opiates and dopamine in the nigrostriatal pathway (Urwyler and Tabakoff, 1981). It has also been suggested that glucose levels are important in regulating the sensitivity of the opiate receptors involved in feeding (Morley et al., 1983). Thus, opiate peptides may contribute to the onset of feeding under certain conditions.

THE ROLE OF FEED INTAKE IN THE REGULATION OF ENERGY BALANCE

The mechanisms involved in receiving information from the periphery and then processing it centrally to produce an appropriate response are not adequately defined. Factors such as GI conditions, hormones, and metabolites act on receptor systems which essentially transduce analog information (e.g., concentration) into neuronal units. Due to the changes in individual neuronal firing that interface with a detector cell and spike a potential generator, e.g., temperature receptor (Edinger and Eisenman, 1970), as well as the number of detector neuron units that are influenced, subsequent changes in the output of a single type of detector system may occur (see Figure 1-1). The final result of such a system is a transformation of analog to digital information (firing rate × number of cells influenced).

The analog information, including sensory inputs, is evaluated and integrated primarily in the hypothalamic area that initiates the appropriate behavior. Specific hypothalamic areas that appear to be important components in the control of feeding and the regulation of energy balance have been identified. For example, stimulating the VMH generally has an inhibitory effect on feeding, and lesions in this area can result in hyperphagia and obesity (Hoebel and Teitelbaum, 1966). The lateral hypothalamus appears to be responsible for the initiation of feeding, with lesions of this area resulting in aphagia and weight loss (Teitelbaum, 1961).

Not only do specific brain areas have an influence on feeding but neural transmitters have been identified as having roles in eliciting and suppressing feeding behaviors (Baile and Forbes, 1974). When injected into specific sites of the hypothalamus of sheep, several putative neurotransmitters, such as norepinephrine, elicited feeding (Baile, 1974). Other experiments on sheep and cattle have shown that several neurotransmitters (Baile et al., 1974b; Forbes and Baile, 1974; Simpson et al., 1975), prostaglandins (Baile et al., 1974a), and certain Ca^{++} and Mg^{++} concentration shifts (Seoane and Baile, 1973, 1975) elicit large meals in satiated animals.

In addition to the factors previously discussed, other factors are involved in feeding behavior and energy balance regulation. The effects of diet dilution can have an influential role on feed intake. Conrad et al. (1964) did a comprehensive study on the effect of availability of en

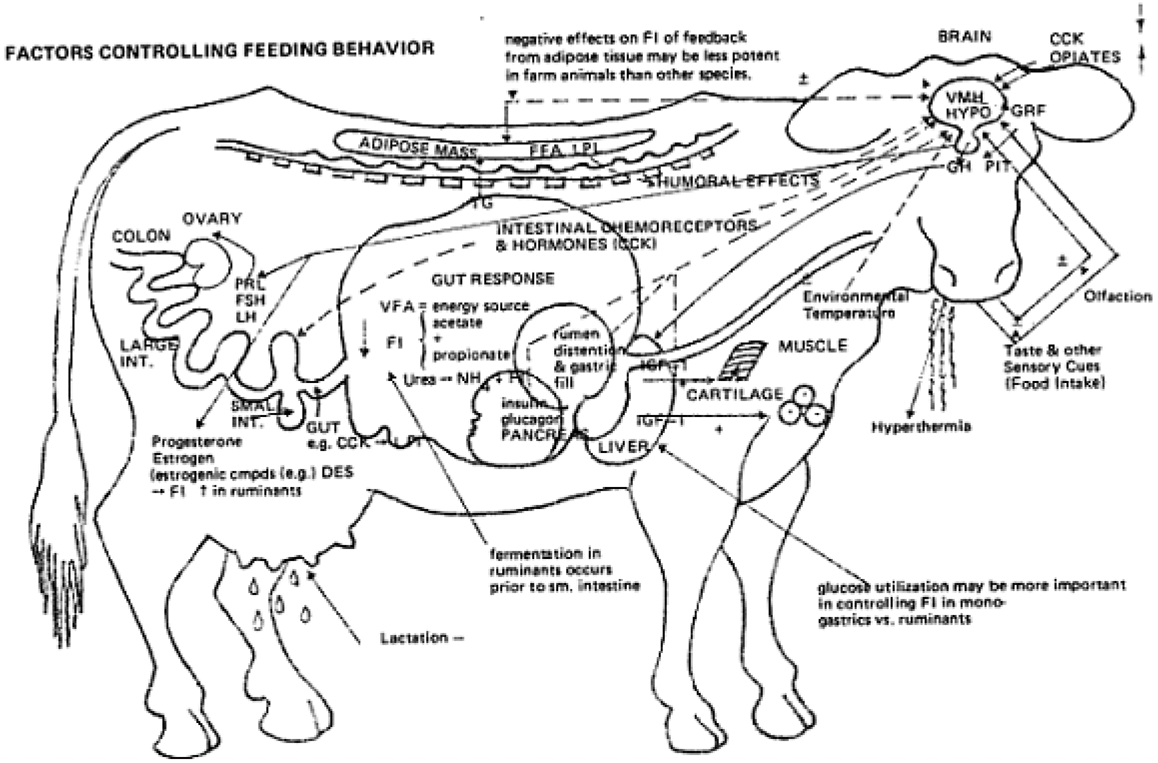

Figure 1-1 Factors controlling feeding behavior. Several factors that influence the control of feeding behavior in the ruminant are summarized. Some differences that exist between species are indicated. The abbreviations and their meanings are: CCK, cholecystokinin; DES, diethylstilbestrol; DHEA, dehydroepiandrosterone; FFA, free fatty acids; FI, feed intake; FSH, follicle-stimulating hormone; GH, growth hormone; GRF, growth hormone-releasing factor; HYPO, hypothalamus; IGF, immunoglobulin factor; LH, luteinizing hormone; LPL, lipoprotein lipase; PIT, pituitary; PRL, prolactin; VFA, volatile fatty acids; and VMH, ventromedial hypothalamus.

ergy from feeds on feed intake in dairy cows. In their study, which examined rations varying in roughage and concentrate content, a number of assumptions were made in accounting for variation between cows. Yet they demonstrated that lactating cows compensate for the dilution of digestible energy (DE) if digestibility of dry matter of the feed was above 67 percent. A relationship between minimum calorie density of diet fed to dairy cows and milk production indicates that the greater the milk production, the more dense the required diet (Bull et al., 1976). These examples illustrate that lactating cows, like sheep and growing cattle, are capable of controlling intake to maintain a constant DE level, provided that the diet has a DE concentration above the critical point. This critical point is variable, depending upon the physiological demands for substrate.

The lipostatic hypothesis suggests that for mature animals to maintain a relatively stable body weight, feed intake must be controlled to regulate total body fat content (Kennedy, 1953). The mechanisms responsible for body fat regulation are not completely understood. Studies in which parabiotic rats were used suggest that a bloodborne factor influences a central control mechanism of the state of the peripheral energy stores (Hervey, 1959). The central control system then modifies feed intake to compensate for shifts in energy balance away from equilibrium. In addition, it is not adequately understood how the state of the lipid depot may influence energy balance regulation in the ruminant. It may be related to the selection for certain traits of the animal, i.e., the "finish" which is in part related to fatness that varies among species and breeds of animals. Such differences may be the result of changes in the level at which fat depots are regulated. There is evidence that fat ruminants consume less than thin ones and may regulate their fat depots (Baile and Forbes, 1974; Paguay et al., 1979). From the evidence that exists it appears that a humoral factor may be one link between lipid depots and the CNS. The level of intake of digestible energy has been shown to be related more closely to weight of body fat than to feed quality (Lee, 1974; Blaxter, 1976). This implies that some physical effect of fat on intake is not sufficient to explain its physiological effects. Forbes (1980a) suggested two ways, unrelated to the set-point theory for body weight, in which fat and fattening might influence the homeostatic balance of energy. First, there is a limit to the rate at which adipose tissue is able to synthesize triglycerides. Smaller amounts of the available excess energy are taken up by adipose tissue as this limit is approached. Those receptors that are sensitive to energy availability recognize the excess and depress intake. Second, the decrease in metabolite uptake by adipose tissue may exert a negative feedback on the energy-sensing centers causing a decline in feed intake.

Substances derived from the ingested feed increase protein and fat synthesis which in turn generate negative-feedback signals to the CNS energy balance regulator. One such substance is a protein deposition promoter, somatomedin. The energy balance regulator provides an input to the controller of hunger and satiety, and thus shifts in the body energy status are reflected by changes in feeding behavior. Deficits in body energy stores modulate the controller to increase meal size and meal frequency, whereas decreases occur during energy surfeit. This substrate uptake is then modulated in the various tissues, i.e., by lipoprotein lipase in adipose tissue and somatomedin in muscle tissue. Consequently, lipoprotein lipase and somatomedin are potential candidates that influence the feedback signal for this energy balance regulator.

It appears that the negative effects on feeding of the feedback from adipose tissue are less potent in domestic farm animals than in other species because of elevated levels of body fat achieved after extended ad libitum feeding (Blaxter, 1976). Forbes (1977) has suggested that this may be related to past selection for fast growth rates without great consideration for carcass composition and a decrease in sensitivity of satiety neurons in the hypothalamus.

SUMMARY

Changes in peripheral or central factors can modify normal feed intake and influence the systems that control hunger and satiety with subsequent effects on production performance. Depending upon environmental conditions under which species evolved, differences exist among feeding behaviors. Among the numerous factors, hormones have received special attention, although the proposed role(s) of any particular hormone has varied over time. Several classes of hormones have been considered in this chapter; among them are GI, pancreatic, and brain peptides (see Table 1-1). Of these classes, a few have obtained notable recognition for their likely roles in the control of feeding. Glucagon of pancreatic origin appears to be involved in satiety. Another pancreatic hormone considered for its role in the control of feeding is insulin. Recently, some evidence points to the possibility that CSF insulin-like factors provide an integrated link between the metabolic state of the adipose tissue and the brain structures involved in the control of feeding. Thus, these may be primary hormones for the maintenance of energy balance or body weight.

Studies with two classes of peptides, CCK and opiate peptides, have shown that these may play a role in controlling feed intake. CCK, an intestinal and brain hormone, appears to act as a satiety agent. The brain opiates are most likely involved in the transmission of information concerned with the interaction of feeding and maintenance of energy balance. Thus, their functions may be interrelated. Other peptides, such as somatomedins, influence growth of nonadipose tissues and may also act on energy balance regulators with a resulting decrease in feeding behavior.

TABLE 1-1 Summary of Factors Influencing Food Intake

Factor	Effect
Sensory	
Olfaction	Controls food intake
Taste	Controls food intake
Temperature	Controls food intake
Brain	
Hypothalamus	Controls energy balance
Pituitary	Controls energy balance
Metabolites and hormones	
Somatomedin	Affects muscle and cartilage
Glucose	Little control of food intake in ruminants; greater control in monogastrics
GH	Decreases insulin: GH[a]; initiates feeding
Insulin	Decreases insulin: GH; initiates feeding
Glucagon	Undefined
FFA	Undefined
Amino acids	None in ruminants
Digestion	
Meal size	Tension receptors detect rumen distension
Diet digestibility	Duodenal receptors detect absorbed nutrients in sheep
Feeding frequency	Affects rate of ingesta passage
H_2O intake	Controls food intake
Fermentation pH	Affects chemoreceptors in rumen wall
Urea	
Urea, ammonium chloride, and ammonium lactate (injections)	Shortens meal length in goats
Urea (as feed additive)	Decreases length of first meal and meal size, but total intake remains unchanged because spontaneous meal number increases in cows
Acetate	Reduces meal size in cattle, sheep, and goats
Lactate (sodium lactate injections)	Reduces meal size in goats
Propionate	Reduces intake; shows evidence of propionate receptors in ruminal vein walls
Sex hormones	
Estrogenic compounds	Increase food intake in ruminants
Progesterone	Affects other ovarian hormones
DHEA[b]	Decreases weight gain without affecting food intake in mice
PRL[c]	Affects lactation and other physiological responses
FSH[d]	Affects lactation and other physiological responses
LH[e]	Affects lactation and other physiological responses

[a] GH, growth hormone.
[b] DHEA, dehydroepiandrosterone.
[c] PRL, prolactin.
[d] FSH, follicle-stimulating hormone.
[e] LH, luteinizing hormone.

Clearly, then, the CNS and its pathways play a primary role in the control of feeding behavior and the regulation of energy balance. The specific actions or components of the associated physiological systems and the interfaces of information remain inadequately defined. Until recently, the emphasis of research has focused primarily on changes in gastric functions as well as the metabolite responses associated with feeding. Now interest has shifted to the influential role of the CNS and various means of modifying voluntary feed intake. With the greater understanding of control systems, it appears likely that feeding behavior and the level at which body energy content is maintained in adult animals, or the rate at which it increases in growing animals, can be modified. Such modifications could lead to improved bioenergetic efficiencies and reduced management demands. In addition, certain metabolic diseases could be prevented if the hunger drive was stimulated sufficiently to compensate for the lacking nutrient supply. These modifications may lead to improved efficiencies and allow greater food and fiber production from animals.

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2

Fishes

INTRODUCTION

The farming of fish is a comparatively recent development in animal agriculture, and present feeding practices reflect this fact. Traditionally, the amount of feed offered fish has been based on a percentage of body weight adjusted by the length of the fish, the water temperature, and an anticipated feed conversion ratio (Buterbaugh and Willoughby, 1967; National Research Council [NRC], 1981). It was difficult to feed fish ad libitum until the more recent development of demand feeders—excess feed was either carried away by the flowing water or it disintegrated to the point that it was unavailable to the fish while it simultaneously competed for the available dissolved oxygen. Ad libitum or demand feeding has now become more practicable because of the development of demand feeders that can dispense small volumes of feed when activated by the fish. These feeders have found wide acceptance in the fish farming industry because they reduce the labor required for feeding and result in improved growth (Boydstun and Patterson, 1980). Also, as more data on digestibility and metabolizable energy of feeds become available (NRC, 1981, 1983), feeding levels can be more accurately predicted. In this chapter, voluntary feed intake refers to feed consumed by fish when it is available at all times or when fish are fed to satiation at frequent intervals.

Generalizations are difficult when one attempts to describe the factors that affect feed intake in fishes; they are an extremely numerous group, representing more than half of all vertebrate species and are, accordingly, a group with great latitude for variation. Carp and goldfish (both cyprinid fishes) are as anatomically and physiologically different from trout and salmon (both salmonid fishes) as the pig is from the cow. Fishes have also adapted to an enormous variety of environments. Their feed intake, within a genus, is determined largely by metabolic rate, which is directly proportional to the temperature of the water in which they live. The phylogenetic system of classifying fish according to anatomical development is also misleading—especially if one is considering the same species raised in the wild as opposed to a controlled environment. Another system of classifying fishes that is more appropriate for the present review is one that separates them into groups according to the degree of control that man exerts over their rearing and propagation. Wild fish reproduce, grow, and die in natural rivers, lakes, and streams in fresh or salt water and are never removed from this environment or restricted in any manner; their feeding and survival depend on the environment and their own instincts. The second group, which lies between the wild and cultured groups, includes fishes used for the restoration or maintenance of a sport fishery. These are partly dependent on external factors in their environment, as they are spawned, hatched, and grown to stockable size in a controlled environment (hatchery) and then are released into a natural environment where they must again become dependent on their instincts for survival. Cultured fishes grow in a controlled environment and are completely dependent on external factors for survival. This group may be subdivided into aquarium fishes, which are cultured specifically for the fish hobbyist or medical-biological researcher, and food fishes (e.g., trouts, catfishes, eels, and carps), which are intensively grown to a desired market size by applying husbandry techniques not unlike those used with domestic farm animals.

Little basic research into the environmental, physiological, and dietary factors that affect feed intake in fishes has been accomplished, despite the modest amount that has been published on the nutritional requirements of fishes (NRC, 1981, 1983). Also surprising is the lack of scientific objectivity in the published research on estimates of food consumption of wild fish.

Because the worldwide populations of wild fishes are diminishing, it is important to determine whether the density and age structure of a population are in proper balance with available food resources. If a fish population is to be effectively managed for optimum production, its food consumption must be accurately estimated. Two basic approaches have been used in this type of research. In one, field data on stomach contents are converted into estimates of daily food consumption; the second involves data developed from laboratory experiments on feeding or metabolism extrapolated to field conditions. Both approaches have been severely criticized since the usefulness of the data they yield is limited with respect to size and age classes, temperatures, and seasons. Methods based on stomach contents, besides being laborious, do not indicate how food consumption might be expected to change with changing environmental conditions or food availability. Furthermore, it can be argued that extrapolations from laboratory studies on food intake and growth are not valid because the feed intake of fish in nature is directly dependent on food availability. The amount of energy expended on foraging activity is also a significant item in determining feed intake and feed utilization efficiency.

The review in this chapter encompasses the published research as it relates to factors that affect feed intake in cultured fishes. Such a review is reasonable, since results extrapolated from studies with wild fishes are of doubtful validity; it is justifiable because many of the valuable natural fisheries have been overexploited (NRC, 1981). The harvesting of larger amounts of fish from the seas and inland waters does not appear promising because the costs of equipment and effort far exceed prospective additional fishery yields. Furthermore, the supply and demand situation for desirable fish is rapidly changing, and production by fish farming or aquaculture has become progressively more feasible.

Most factors known to modify feed intake in fish can be characterized as environmental, physiological, or dietary. It should be remembered, however, that many of the environmental factors that modify feed intake cannot be isolated from the physiological and dietary factors and vice versa.

ENVIRONMENTAL FACTORS

Water temperature, chemistry (including pH), velocity, as well as photoperiod are all ecological determinants of feed intake in fishes. Brocksen and Bugge (1974) investigated the influence of temperature on feed intake in rainbow trout (*Salmo gairdneri*) and reported that intake increased with temperature from 5°C to 20°C. Below 5°C, feeding activity was very little or nil. Wallace (1974) found that the tropical blenny (*Blennius pholis*) ate 1.8 times as much food at 25°C as at 10°C. It is clear that different species of fish have different physiological optimum temperatures and that temperature changes do not equally affect the voluntary feed intake. In rainbow trout, brown trout (*Salmo trutta*), and sock-eye salmon (*Oncorhynchus nerka*) these optimum temperatures are 17°C, 13°C, and 15°C to 17°C, respectively (Storebakken et al., 1981). Some species of fish live and grow in arctic and antarctic waters where body temperatures are at or below the freezing temperature of freshwater, while other species thrive in hot springs with body temperatures as high as 40°C (Sumner and Lanham, 1942). By contrast, the tolerable body temperature range for homeotherms is only a few degrees (Brody, 1945). Adaptations have been made over a wide range of temperatures by fishes, with each species having a preferred temperature at which voluntary feed intake is highest.

Studies on the effects of water chemistry on feed intake seem to be limited to situations with various water salinities. Most are confounded with such variables as temperature and food availability. One study in which conditions were standardized and food intake was measured was reported by MacLeod (1977). Working with rainbow trout acclimated to various salinities and temperatures, MacLeod showed that feed intake was highest at the intermediate water salinities from 15.0 to 28 ‰, lower in freshwater and 7.5 salinity, and lowest (by a statistically significant margin) at 32.5 salinity. Food intake was adversely affected by sudden changes in salinity in either direction. MacLeod speculated that "the increased feed intake recorded in salinities from 7.5 to 28 could be exploited to increase the throughput of rainbow trout production in fish farming operations."

Frequency of feeding is important; small trout are fed as often as 10 to 24 times per day (NRC, 1981). The frequency is gradually reduced to one to three times per day as the size of the fish increases. Murai and Andrews (1976) showed that the growth of channel catfish (*Ictalurus punctatus*) weighing less than 1.5 g was fastest when the fish were fed eight times daily. Feed intake decreased from about 10 to 5 percent of body weight as the fish grew, suggesting that the high frequency of feeding requirement by small catfish is related to their high feed intake rate. Luquet et al. (1981), in a series of experiments with rainbow trout, showed that both frequency of feeding and length of fasting periods markedly affected feed intake and weight gain. Weight gains were significantly lower in groups of trout fed once a day than in those fed more than once a day. Total feed intakes on the day of refeeding after fasts of varying lengths (1 day to 1 week) did not differ significantly. A compensatory increase in feed intake after a fast was limited to the first meal on the day that feeding resumed; thereafter the level of intake was low.

Feed intake, as well as growth, can sometimes be accelerated by increased photoperiod (Komourdjian et al., 1976). Daylight affected the feed intake of Dover sole (*Solea solea*) and dab (*Limanda limanda*), whereas tidal cycles were more important in a blenny (Krunk, 1963; Jobling, 1974; Crawford, 1977). Food consumption of green sunfish (*Lepomis cyanellus*) was highest after exposure to 8 to 16 h of light per day (Brett and Groves, 1979). The above findings support the conjecture that photoperiod effects are probably mediated via the hypothalamic pituitary axis and are expressed as changes in the production or release (or both) of growth hormone.

Factors such as oxygen and ammonia concentrations in water have a marked and predictable effect on feed intake. Lowered dissolved oxygen and elevated ammonia in water lead to a diminution in feed intake in cultured fishes under otherwise identical environmental conditions (Haskell, 1959).

Fish have pronounced effects on each other when they feed in groups, even when unlimited feed is available. When among fish of the same species, each fish tends to consume less feed than when fed alone (Mann, 1967). It has been speculated that the proximity of two or more fish of the same species stimulates each to increase its rate of feeding, probably due to competition. Antithetically, Kinne (1960) found a reduction in feed intake due to increased stocking density with highly territorial fishes. He postulated that the accumulation of metabolic ammonia and lower dissolved oxygen depressed metabolism and the resultant feeding activity.

PHYSIOLOGICAL FACTORS

Although physiological stimuli are among the most important factors governing feed intake of higher vertebrates, they have received only scant attention in fishes.

According to studies by Thorpe and Morgan (1978), different populations of Atlantic salmon (*Salmo salar*) demonstrated that genetics are not a determinant in feed intake. They showed that feed intake and growth response occurred at the same ratio of food particle size to fish length, irrespective of family group. Since the general relationship between growth and this ratio was common to all groups tested, they concluded that "it was unlikely the relative effect of feed size was influenced by differences in the genetic background of the fish."

The amount of food eaten in a day is often expressed as a percentage of the body weight of the fish. This is interesting when one considers the wide range of weights encountered during the feeding period. Trout weigh about 150 mg when they start feeding and usually are grown to a weight of about 500 g. This 3,000-fold increase in weight is considerably more than the potential weight increases in most mammals. The percentage of food eaten in relation to body weight decreases as weight increases, because small fish have a higher metabolic rate and thus require more food per unit of weight than do larger fish (NRC, 1981). Brett (1971) found that the daily feed intake of young sockeye salmon held at 15°C decreased from an average of 16.9 percent of the dry body weight for a 4-g fish to 4.5 percent for a 216-g fish. Young chinook salmon (*Oncorhynchus tschawytscha*), weighing 0.6 g, consumed up to 20 percent of their dry body weight per day (Davis and Warren, 1968) at 10°C. Elliott (1975) reported a value of 16.4 percent for a 1-g brown trout held at 18°C. On a dry food to wet body weight basis, feed as a percentage of body weight can vary between 0.5 and 10.0 percent for growing fishes, depending on water temperature and chemistry (NRC, 1981, 1983). The causal effect of increasing size or age to decreased feed intake can only be pondered at this time. These factors are probably related to changes in the endocrine and metabolic functions of the fish. Peter (1979) showed that the neural aspects of feed intake control in fishes are similar to those of higher vertebrates. Even though lesion and electrical stimulation techniques have been successfully used to locate the brain regions involved with feeding behavior (e.g., hypothalamus and other brain glucoreceptors), clear interpretations of such studies have not been possible. Fletcher (1984) suggested that an important consideration is the fluctuations of plasma metabolite levels that have been associated with changes in feed intake and the role of select neural regions in their regulation.

Several hormones have been shown to affect feed intake in fishes. A number of fish species show periodic depletion and repletion of carcass energy reserves that can be linked with seasonal changes in hormone secretion (Higgs et al., 1982). It is widely recognized that a number of fish species cease feeding during the reproductive season. Such periods are linked to changes in feeding behavior and occur in connection with migration as well as with reproductive cycles. Higgs et al. (1982) and Fletcher (1984) have suggested that hormones may influence hunger indirectly by affecting the secretion of other hormones or by inducing changes in the levels of various plasma nutrients.

Donaldson et al. (1979) and Higgs et al. (1982) summarized the published literature concerning the effects of thyroid hormones on fish growth and, indirectly, feed intake. There is some evidence that thyroid hormones increase the rate of absorption of some nutrients across the gut, thereby enhancing feed conversion efficiency and fish growth. The maintenance of adequate thyroid status in fishes is regarded as a prerequisite for normal growth. The major thyroid hormone effect may lie in its potentiating action on other anabolic hormones, most notably growth hormone.

Steroid hormones (both androgens and estrogens) have been shown to either suppress or enhance appetite in fishes while simultaneously altering plasma nutrient levels (Yu et al., 1979; Ince et al., 1982). Donaldson et al. (1979) showed that growth of fish may be stimulated by at least 14 of the known androgen-anabolic steroids that are effective in mammals. Most, if not all, of these steroid hormones increased feed consumption while they improved feed conversion efficiency and dietary protein utilization. Markert et al. (1977) and Chua and Teng (1980) showed that the use of bovine growth hormone in fish substantially improved feed intake and increased growth, while it concurrently lowered production costs. Hormones such as prolactin have been shown to affect diurnal variations of plasma fatty acids in Pacific salmon (Peter, 1979). High blood levels of free fatty acids may suppress feed intake, as they do in higher vertebrates. The activity of prolactin may be entrained by either thyroxine or cortisol; and circadian rhythms in the plasma levels of a number of hormones, including prolactin, thyroxine, and growth hormone, have been observed in some species (Meier, 1970; de Vlaming and Sage, 1972). It seems highly likely that feed intake is affected by such endocrine activity.

Murat et al. (1981) observed that a variety of fish species showed appreciable changes in plasma insulin levels in response to fluctuations in plasma nutrients. However, the possible influences of insulin and other hormones (i.e., cholecystokinin, cerebrospinal fluid insulin) associated with feed intake and nutrient assimilation remain to be investigated.

Stomach fullness and systemic factors such as circulating nutrients and respiratory rate have been shown to be closely related to feed intake (Muir and Niimi, 1972; Ware, 1972; Lee and Putnam, 1973; Toates, 1981). Grove et al. (1978) found that when food of decreased energy content per unit weight is presented to trout, the compensation which follows to increase daily intake is an increase in the rate of feeding along with a demonstrable decrease in gastric emptying time. Even though it is reasonable to assume that feeding activity ceases when the stomach is full, the total feed intake by some fish species has been observed to be limited by the specific gravity of the feed (Lovell, 1979).

DIETARY FACTORS

Nutrient Deficiency

Many examples in the literature relate reduced feed intake to a nutrient deficiency in the diet (NRC, 1981, 1983). For instance, a deficiency of thiamin or zinc can cause anorexia. It is not known whether these depressions of intake are primary or secondary, but it is understood that the lack of an essential nutrient causes a deterioration in general health, which in turn would affect feeding behavior. Jobling (1983) speculated, without supporting data, that dietary energy concentrations (total, digestible energy [DE], or metabolizable energy [ME]) are more important than specific nutrients in the regulation of food consumption. Lee and Putnam (1973) showed that the daily feed intake increased when the energy content of the available food decreased. It is generally held that fishes eat to satisfy their energy requirements and that metabolizable energy is the main factor limiting feed intake (NRC, 1981, 1983; Bromley and Adkins, 1984).

Food Particle Size and Composition

Feed intake and growth rate have been shown to be closely related to food particle size (Wankowski, 1977; Wankowski and Thorpe, 1979). Optimum particle size in Atlantic salmon increased in direct proportion to fish length. Growth was fastest in Atlantic salmon finger-lings given feed with particle diameters equal to 2.2 to 2.6 percent of body length. At particle sizes corresponding to 6.8 percent of body length, feed ingestion ceased. Furthermore, it was demonstrated that fishes select against feed particles with diameters less than 2.2 percent of body length. Wankowski speculated (based on morphometric measurements of mouth breadth and gill raker spacing) that these results could be extrapolated to marine fishes.

The use of pelleted (compressed) and extruded (expanded) diets in fish farming has led to the establishment of empirical rules relating to the size of pellet to be fed to fish of a particular size class. Recommendations have been based largely on experience rather than on experimentation (Table 2-1). Although particle size plays a major role in acceptance or rejection of a diet, it is much more critical for dry diets than for semimoist or moist diets (NRC, 1981).

Poston (1974) found that brown trout fed diets containing 10 to 55 percent moisture at similar rates, when adjusted for dietary moisture, had comparable dry matter intakes. Likewise, Bromley (1980) fed turbot identical amounts of dry matter in a ration ranging from 0 to

74 percent water. Dry matter intake was the same and he, like Poston (1974), concluded that water content was immaterial as long as the basic nutrient requirements were met. It has been reported that fry of chinook salmon apparently accept moist diets better than air-dry feeds (NRC, 1983). Although the reason for this preference is unknown, it has been suggested that the ability to incorporate water into the ingesta differs among different fishes.

TABLE 2-1 Food Particle Size Recommendations for Trout

	U.S. Series (Sieves)[a]				
Granule Pellet Size	Effect on Feed[b]	Screen Opening Size	Standard No.	Fish Size (g)	
				Begin	End
Starter	Through	595 μm	30	—up to	0.2
	Over	420 μm	40		
#1 Granule	Through	841 μm	20	0.3	0.5
	Over	595 μm	30		
#2 Granule	Through	1.19 mm	16	0.6	1.8
	Over	841 μm	20		
#3 Granule	Through	1.68 mm	12	1.9	4.5
	Over	1.19 mm	16		
#4 Granule	Through	2.83 mm	7	4.6	15.0
	Over	1.68 mm	12		
	Diameter (mm) Length (mm)				
3.18-mm pellet		3.18 × 3.18		15	45
4.76-mm pellet		4.76 × 4.76		46	150
6.35-mm pellet		6.35 × 6.35		151	—

[a] From the National Bureau of Standards.

[b] For example, starter particles will sift through a 595 μm (30) screen; the particles will rest on top of a 420 μm (40) screen. SOURCE: NRC (1978).

Feeding Stimulants

In terms of control of feed intake in fishes, olfactory and gustatory stimuli have received the most attention by researchers. Although food may be detected at a distance either visually or chemically by fish, the final decision about whether to swallow or reject potential food material is based on gustation (Adron and Mackie, 1978). The feeding behavior of several species of marine and freshwater fishes was found to be mediated by mixtures of chemicals, implying that a number of different chemosensory cells must be stimulated to induce a feeding response (Mackie et al., 1980). The mixtures that cause the greatest behavioral responses are composed of amino acids, nucleotides, and quaternary amines. Among the single compounds that show the highest effectiveness in these mixtures are betaine, glycine, alanine, and taurine. Feed intake in Dover sole was shown by Mackie et al. (1980) to be markedly stimulated by betaine alone in larger (> 50 g) fish and by betaine plus glycine or alanine in smaller (about 2.5 g) fish.

Betaine plus mixtures of amino acids are feeding stimulants for the pinfish (*Lagodon rhomboides*), pigfish (*Orthopristis chrysopterus*), and puffer fish (*Fugu perdalis*) (Carr and Chaney, 1976; Carr et al., 1977; Ohsugi et al., 1978). Glycine was a particularly strong attractant for flounder (*Pseudopleuronectes americanus*) (Sutterlin, 1975). Two dipeptides, hypotauryl-2-carboxyglycine and *C*-methylimino-diacetic acid, were active feeding stimulants for grunt (*Bathystoma rimator*) (Sangster et al., 1975). Mackie and Adron (1978) demonstrated that the turbot (*Scophthalmus maximus*) showed a strong gustatory sensitivity to specific nucleotides such as inosine and inosine 5'-monophosphate. Mixtures of amino acids were effective feeding stimulants for rainbow trout (Adron and Mackie, 1978). Rainbow trout that were trained to use demand feeders showed a marked preference for a diet that contained all synthetic amino acids and that simulated the amino acid profile of squid muscle over a plain casein diet with an amino acid profile based on known requirements. When amino acid D-forms were substituted for the L-forms, the resulting diet was repellent, thus indicating a possible stereospecificity at the receptor surface. Individual amino acids were either without effect or repellent. When the amino acid mixture was arbitrarily divided into several fractions, feeding activity was greatest in fish fed the aromatic and basic amino acid fractions. Two aromatic amino acids, tyrosine and phenylalanine plus either lysine or histidine, were highly stimulatory. No other combination of these amino acids was effective, and in fact, phenylalanine, lysine, and histidine were repellent. When certain individual amino acids or combinations were shown to be repellent, fish usually took the pellet into the mouth and then rejected it. This behavior suggests that if olfaction were the main sense involved, the repellent diet would be rejected before it was mouthed. Gob and Tamura (1980), working with bream (*Chrysophyrys major*), found the rank of feeding behavior response to the best 7 of the 15 compounds tested was as follows: alanine-betaine > glycine-betaine > L-alanine > L-valine > L-serine > L-arginine > L-glutamine. The behavioral responses were consonant with electrical physiological measurements of the gustatory system. Goh et al. (1979) speculated that taste responses to amino acids are species specific while olfactory responses are not.

Feed Quality

Feed quality, including the presence of adventitious toxins, is readily detectable by fish (NRC, 1981, 1983).

The inclusion of oxidized fish and vegetable oils in fish diets results in reduced feed intake. Substances like gossypol in cottonseed and protease inhibitors in soybean meal cause anorexia when they are present in feed-stuffs used in fish feed manufacturing. Aflatoxins and T-2 toxins, which are produced by different molds growing on feedstuffs, depress feed intake (NRC, 1981; Poston et al., 1982). Finally, there is much evidence that manmade contaminants—as typified by industrial chemicals, pesticides, and herbicides—sometimes lead to depressed appetite as well as a myriad of metabolic disorders (NRC, 1983).

PREDICTING FEED INTAKE

Quantitatively, the most important factors regulating the amount of feed consumed by fishes are species, body temperature (which is close to water temperature), body weight, feed DE content, feed palatability, and particle size. Table 2-2 was developed by Hilton and Slinger (1981) and used by the NRC (1981) in its report on cold-water fish nutrient requirements. Table 2-2, the feeding guide publication of Buterbaugh and Willoughby (1967), and the feeding guide recommendations of several feed manufacturers (unpublished) have been used to derive some feeding equations for rainbow trout. The mathematical derivation of these equations required that the following assumptions be made:

1. The metabolic body size and the feed energy requirement of fish is proportional to the 0.75 power of body weight ($BW^{0.75}$) (Smith et al., 1978).
2. The length-weight relationships for salmonid fish published by Piper et al. (1982) are correct.
3. A growth rate of 1 in. (2.54 cm) per month is acceptable growth for rainbow trout at 15°C (Piper et al., 1982).
4. Feed containing 3,000 kcal of DE/kg will produce fish at a conversion efficiency of 1.5 g of feed/g of growth (NRC, 1981).
5. The finding by Haskell (1959) that "the normal growth of trout under conditions of constant water temperature and adequate food supply is such that the rate of increase in body length is constant" is correct.
6. The effect of temperature on metabolism and the feed (energy) requirement of trout is linear in the range of temperatures usually encountered in salmonid production (6°C to 18°C) (Iwama and Toutz, 1981).

Feeding Equation Derivation

A 100-g fish in 15°C water growing at the rate of 1.4 percent per day will gain 1.4 g/day. At a feed conversion ratio (feed/gain) of 1.5 g of feed/g of gain, this requires 1.4 × 1.5 = 2.1 g of feed/fish/day, which is equal to 2.1 percent BW. However, metabolic body size and feed requirement is proportional to $BW^{0.75}$, e.g.,

$$\frac{\text{Amount of feed/fish}}{BW^{0.75}} = K\frac{2.1}{100^{0.75}} = 0.0664.$$

This procedure was repeated for several sizes of fish ranging in weight from 12 to 180 g, and a constant (*K*) with a (rounded-off) mean value of 0.066 was obtained and used to calculate feed intake using the following simplified equation:

$$\text{Amount to feed (\% BW)} = 0.066BW^{-0.25}100. \qquad (1)$$

TABLE 2-2 Fish Feeding Guide

Number of Fish/kg	Granule and Pellet Size, in. (mm)	% BW Consumed per Day at the Following Water Temperatures (°C)									
		6	7	8	9	10	11	12	13	14	15
2,600	#1	2.9	3.4	3.7	3.9	4.6	4.8	5.2	5.8	6.0	6.4
1,300	#1	2.8	3.3	3.6	3.8	4.4	4.7	4.9	5.6	5.9	6.1
700	#2	2.7	3.0	3.3	3.6	4.1	4.5	4.8	5.1	5.6	5.8
400	#2	2.6	2.8	3.0	3.2	3.9	4.0	4.6	4.9	5.0	5.1
200	#3	2.3	2.6	2.8	3.0	3.6	3.8	4.3	4.5	4.6	4.7
130	#3-4	2.1	2.3	2.5	2.8	3.3	3.6	3.7	3.9	4.0	4.1
90	#4	1.9	2.0	2.1	2.4	2.7	2.9	3.0	3.2	3.6	3.8
40	3/32 (2.4)	1.6	1.7	1.8	1.9	2.0	2.1	2.4	2.6	3.0	3.2
30	3/32 (2.4)	1.5	1.6	1.7	1.8	1.8	1.9	2.0	2.2	2.8	2.9
20	1/8 (3.4)	1.3	1.4	1.5	1.6	1.7	1.8	1.9	2.1	2.4	2.5
15	1/8 (3.4)	1.2	1.3	1.4	1.5	1.6	1.7	1.8	2.0	2.3	2.4
10	3/16 (4.8)	1.1	1.2	1.3	1.4	1.5	1.6	1.7	1.8	1.9	2.0
5	3/16 (4.8)	1.0	1.1	1.2	1.3	1.4	1.5	1.6	1.7	1.8	1.9
2	1/4 (6.4)	0.8	0.9	1.0	1.0	1.1	1.1	1.2	1.3	1.5	1.6

NOTE: Feeding rates are based on a single strain of rainbow trout fed dry diets containing digestible energy of approximately 3,000 kcal per kg (J. W. Hilton and S. J. Slinger, University of Guelph, Guelph, Ontario, Canada, personal communication, 1979).
SOURCE: NRC (1981).

TABLE 2-3 Comparison of Recommended Feeding Levels (Percent of BW to Feed/Day) for Rainbow Trout at 15°C

Fish Size							
						Calculated[e]	
Length (in., cm approx.)	Weight (g)	H & S[a]	Rangen[b]	Murray[c]	B & W[d]	DE (3,200)	DE (3,000)
	0.250	—	—	—	—	9.1	—
	0.385	6.4	6.5	—	11.8	8.1	8.7
	0.5	—	—	—	—	7.6	—
	0.770	6.1	6.0	—	9.4	6.8	7.3
2 (5.1)	1.43	5.8	5.8	7.8	7.4	5.9	6.3
	2.50	5.1	5.2	6.5	6.2	5.1	5.4
3 (7.7)	5.00	4.7	5.0	6.0	5.0	4.3	4.6
	7.70	4.1	4.3	5.2	4.3	3.9	4.1
4 (10.2)	11.1	3.8	3.9	4.9	3.8	3.5	3.7
5 (12.7)	25.0	3.2	3.3	4.0	3.0	2.9	3.1
6 (15.2)	33.3	2.9	3.0	3.5	2.6	2.7	2.8
	50	2.5	2.7	3.1	2.4	2.4	2.6
7 (17.8)	67	2.4	2.6	2.7	2.2	2.2	2.4
8 (20.3)	100	2.0	2.2	2.4	1.8	2.0	2.2
10 (25.4)	200	1.9	1.8	1.8	1.6	1.7	1.8
	500	1.6	1.6	1.3	—	1.4	1.5

[a] Hilton and Slinger (1981).

[b] Rangen, Inc.

[c] Klontz et al. (1985).

[d] Buterbaugh and Willoughby (1967).

[e] Calculated by Equation 4. Numbers in parentheses are DE kcal/kg.

It is generally held that, within the range of the physical capacity of the digestive system, fish will eat to meet their energy needs. It has been determined by many years of hatchery experience and research studies that diets which contain 3,000 kcal of DE/kg will allow trout to convert feed to flesh at about 1.5 feed conversion value. To introduce the energy value of feeds, Equation 1 is multiplied by 3,000 and divided by the DE of the diet being fed:

$$\text{Amount to feed (\% BW)} = \frac{0.066\text{BW}^{-0.25}3{,}000}{\text{DE}} = \frac{200\text{BW}^{-0.25}}{\text{DE}}. \quad (2)$$

TABLE 2-4 Comparison of Recommended Feeding Levels (Percent of BW to Feed/Day) for Rainbow Trout at Three Water Temperatures and Five Different Fish Sizes

						Calculated[e]	
Temperature (%)	Fish Weight (g)	H & S[a]	Rangen[b]	Murray[c]	B & W[d]	DE (3,200)	DE (3,000)
6	1.4	2.7	3.9	2.8	1.3	2.6	2.7
6	5.0	2.3	3.1	2.0	0.8	1.9	2.0
6	25.0	1.6	1.9	1.2	0.4	1.2	1.3
6	50.0	1.3	1.5	0.9	0.3	1.1	1.1
6	100.0	1.1	1.2	0.3	0.3	0.9	0.9
10	1.4	4.1	4.6	4.3	3.3	3.7	3.9
10	5.0	3.6	4.0	3.6	2.1	2.7	2.8
10	25.0	2.0	2.6	2.2	1.3	1.8	1.9
10	50.0	1.7	2.0	1.7	1.0	1.5	1.6
10	100.0	1.5	1.6	1.4	0.8	1.3	1.3
15	1.4	5.8	5.7	7.8	7.8	5.8	6.1
15	5.0	4.7	4.7	6.0	5.0	4.2	4.5
15	25.0	3.2	3.0	4.0	3.2	2.8	3.0
15	50.0	2.5	2.4	3.1	2.7	2.4	2.5
15	100.0	2.0	2.0	2.5	2.4	2.0	2.1

[a] Hilton and Slinger (1981).

[b] Rangen, Inc.

[c] Klontz et al. (1985)

[d] Buterbaugh and Willoughby (1967).

[e] Calculated by Equation 4. Numbers in parentheses are DE Kcal/kg.

The constant 200 in Equation 2 applies to rainbow trout growing in 15°C water at the rate of about 1 in. (2.54 cm) per month. The constant should be considered a guide and can be modified to fit various rearing conditions. By adjusting this factor up or down, more or less growth can be obtained with some loss of efficiency. A constant that would apply to other species and other growth rates would need to be determined experimentally. Table 2-3 shows a comparison of suggested amounts of feed to be fed according to Hilton and Slinger (1981), Buterbaugh and Willoughby (1967), and two leading feed manufacturers versus those calculated using Equation 2. It is worth mentioning that some newer feeds contain upwards of 4,000 kcal of DE/kg. These higher-caloric-density feeds would be wasted if fed according to existing feeding tables.

Estimates on the quantitative change in feeding due to changes in water temperature range from 5 to 10 percent/°C. However, over the range of temperatures usually experienced in most trout farming operations, the response is nearly linear. For this exercise we have used a rate of feeding change of 9 percent/°C and a modification of the compound growth equation $A_1 = A_0 e^{rt}$, where A_1 is the amount of feed at some future temperature, A_0 is the amount of feed at the present temperature, r is rate, t is time, and e is the base of natural logarithms.

The effect of temperature (Tin °C) on fish feed intake can be calculated by modifying the equation as follows:

$$A_1 = A_0 e^{0.09(T-15)}, \qquad (3)$$

By combining Equation 2 with Equation 3, we can determine the amount to feed (percent BW) at any temperature using the following equation:

$$\text{Amount to feed} = \frac{200\ \mathrm{BW}^{-0.23} e^{0.09(T-15)}}{\mathrm{DE}}, \qquad (4)$$

Table 2-4 shows a comparison of the amounts to feed at three temperatures and five fish body weights from several different sources with those calculated by Equation 4.

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3

Swine

INTRODUCTION

In the United States, growing pigs are allowed to consume feed ad libitum from weaning to the time that they have reached market weight. The feed intake of gilts and boars to be used for breeding is restricted during the latter part of the growing period. Feed intake of the breeding herd is also restricted, except for that of sows during lactation. Therefore, the definition of voluntary feed intake is restricted in this chapter primarily to the growth period and the period during lactation.

Voluntary feed intake is expressed in terms of digestible energy (DE) because this is the energy introduced into the biological system and because this minimizes the effects of energy density on feed intake. As a unit expressing feed intake, metabolizable energy (ME) provides little improvement in comparison with DE because with a balanced diet, ME is about 96 percent of DE and is relatively constant (Agricultural Research Council [ARC], 1981). Many studies have not reported DE concentrations of diets or DE intake, and reported feed intake values have been converted to DE intake by assuming that a corn-soybean meal diet contains 3.2 kcal of DE/g. All references to energy concentration are on an as-fed basis (i.e., 90 percent dry matter). Furthermore, only factors affecting the ad libitum consumption of nutritionally adequate diets are considered.

Because feed costs are 55 to 65 percent of the cost of producing a market pig, feed intake has been recorded in most nutritional studies. In nutritional studies, however, the data are frequently reported for the entire study period or for periods of several weeks. The data are useful for indicating the effects of a dietary factor with reference to a control factor but do not provide insight into the changes in intake that occur on a day-to-day basis.

FEED INTAKE OF GROWING PIGS

Suckling Pig

The feed intake of the suckling, or nursing, pig is dependent upon the ability of the sow to produce milk. Estimates of milk production have been made by isolating pigs from the sow and allowing frequent nursing periods (1-h intervals). Milk production is measured by weighing the suckling pigs before and after suckling and assuming that the gain in weight is a suitable measure of milk intake. This procedure has been described in detail by Lewis et al. (1978).

The summary of experiments reporting solids intake by nursing pigs are derived from milk yield data (Table 3-1). These data suggest that milk yield is maximum by 8 to 15 days after the beginning of lactation and that it remains relatively constant thereafter. Most studies included sows that had completed from two to nine reproductive cycles. O'Grady et al. (1973) reported results from the first, second, and third reproductive cycles and observed an increase in milk yield and milk solids during the second and third reproductive cycles. Litter size was larger, however, and daily intake per pig was not markedly different among lactation periods.

Access to dry feed is frequently provided during the nursing period to supplement the nutrient intake of the nursing pig. During long lactation periods, intake of creep feed may be substantial (Table 3-2). During short lactation periods, however, intake of creep feed is limited. During the second and third week of lactation, intake of creep feed is less than 20 g/day/pig, while 70 to 80 g/day/pig may be consumed during the fourth week of lactation (Okai et al., 1976; Shields et al., 1980; Aherne et al., 1982b). Providing creep feed is of little benefit if pigs are weaned at 3 to 4 weeks of age.

TABLE 3-1 Solids Intake by Nursing Pigs

Day of Lactation	No. of experiments[a]	Daily Solids Intake (kg/pig)			
		Mean	Maximum	Minimum	Standard Deviation
4-8	7	0.111	0.132	0.080	0.019
8-15	20	0.136	0.216	0.090	0.035
16-24	18	0.136	0.195	0.095	0.030
24-41	22	0.131	0.183	0.093	0.022

[a] Results are summarized from the following reports: Aherne and Speer, 1974; Boyd et al., 1982; Coffey et al., 1982; Haught and Speer, 1977; Klaver et al., 1981; Lellis and Speer, 1983; Leonard and Speer, 1983; Lewis and Speer, 1973, 1974, 1975; Mahan et al., 1971; O'Grady et al., 1973; Okai et al., 1976; Rousselow et al., 1979; Rousselow and Speer, 1980; Smith, 1959a,b, 1960,a,b,c, 1961; White et al., 1984.

Based on the data of Okai et al. (1976), Kuan and Mak (1979), and Aherne et al. (1982b), DE intake (DE_i) can be expressed by the following relationship (Figure 3-1):

$$DE_i = 11.2Day - 151.7, \qquad (1)$$

where DE_i is expressed in kcal/day and Day is age of the pig ($R_2 = 0.72$). The standard error of the estimates of the regression coefficient was 1.5 and of the intercept was 35.5. The intake of creep feed is predicted to begin at about 13.5 days of age. Because the data were collected only until day 35, the use of the prediction equation should be restricted to a 5-week lactation period.

TABLE 3-2 Creep Feed Intake by Nursing Pigs

	Age (Days) When:		
Study Reference	Feed Offered	Weaned	Intake (g/day)
Whitelaw et al., 1966	21	56	258.0
Elsley et al., 1969	14	56	245.0
Lodge, 1969	21	56	343.0
Lynch, 1977	10	31	8.5
Haught et al., 1977	10	35	28.4
King, 1979	7	27	47.8
Fowler et al., 1979	10	42	82.0
Shields et al., 1980	14	28	30.0
Corley et al., 1983	14	28	20.8

Weanling Pig

Immediately postweaning (for 2 to 3 weeks), social, physiological, environmental, and dietary stress results in poor feed intake and a reduction in growth rate (Leibbrandt et al., 1975a,c; Okai et al., 1976; Shields et al., 1980; Aherne et al., 1982a; McConnell et al., 1982; Lawrence and Maxwell, 1983; Etheridge et al., 1984). Postweaning growth check and depression of feed intake is less severe as pigs are weaned at an older age (Leibbrandt et al., 1975b). In studies in which feed intake by pigs weaned at 2 to 3 weeks of age has been measured daily, feed intake has been reported to increase linearly or at an increasing rate.

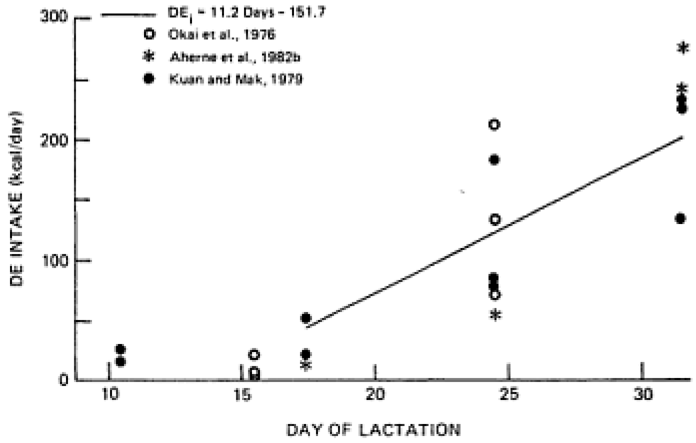

Figure 3-1
Digestible energy intake of creep feed.

McCracken (1980) reported that feed intake of pigs weaned at 10 days of age increased linearly for 28 days at about 23 g/day for diets containing dried skim milk and at about 19 g/day for diets containing cereal grains. McCracken (1981) reported similar linear increases in feed intake of 22 g/day for diets containing dried skim milk and 17 g/day for cereal-based diets. Tullis et al. (1980) reported a linear increase in feed intake of diets of different energy densities of 32 g/day (122 kcal/day) for a high-energy diet and 22 g/day (78 kcal/day) for a low-energy diet by intact male pigs weaned at 21 days of age. Ewan (1983) reported a linear increase in feed intake with corn-soybean meal diets by pigs weaned at 21 days of age. The increase in intake was 32 g/day for a starter diet containing 3.4 kcal/g.

While linear increases in feed intake postweaning have been observed (McCracken, 1980, 1981; Tullis et al., 1980; Ewan, 1983), the total daily intake is limited by the physical capacity of the digestive tract, and therefore the rate of increase must decline as the pig grows. Studies of this portion of the feed intake pattern of the pig have not been reported in detail. Ewan (1983) has summarized experiments that have included 4,597 observations of 1,200 pens of pigs weighing from 5 to 20 kg fed corn-soybean meal diets. The DE content of the diets was assumed to be 3.2 kcal/g. Linear and quadratic regression analysis of the data, removing the effects of pigs or their pens, was conducted with body weight, age, or day of experiment as the dependent variable. The data were best described by the following relationship (Figure 3-2):

$$\mathrm{DE}_i = 462\mathrm{BW} - 9.72\ \mathrm{BW}^2 - 1{,}529, \qquad (2)$$

with DE_i in kcal/day and body weight (BW) in kg. The standard error of the estimate of the linear coefficient was 7.5 and that of the quadratic coefficient was 0.35. The coefficient of determination (R^2) was 0.928. The relationship predicts maximum intake at 23.8 kg BW, with a decline thereafter, and suggests that is useful only at less than about 20 kg BW.

Growing Pig

Headley et al. (1961) described cumulative feed intake of 1,200 pigs fed corn-soybean meal diets in groups of 5 or 10 per pen. The data were used to develop a curve of diminishing increments between body weight and cumulative feed intake. The relationship obtained was:

$$W = A - (A - W_i)\,e^{kf}, \qquad (3)$$

where *W* is the live weight after consumption of *f* pounds of feed, *A* is the maximum weight attainable as a result of growth, W_i is the initial weight at which feeding began, *e* is the base of the natural system of logarithms, and *k* is a constant which determines the decline in efficiency as live weight increases.

Cole et al. (1967a) fed diets varying in DE content from 2.9 to 3.9 kcal/g to eight pigs over the weight range of 38 to 105 kg live weight. The intake of DE was expressed as an exponential function of body weight. The observed relationship for pigs in pens was

$$\mathrm{DE}_i = 575\mathrm{BW}^{0.675}. \qquad (4)$$

DE_i was in kcal/day and was reduced if pigs were in metabolism cages rather than pens. This relationship predicts intake satisfactorily between 30 and 100 kg BW, but it does not provide reasonable estimates if extended beyond the range of the data base.

In a series of reports (DeShazer and Teter, 1974;

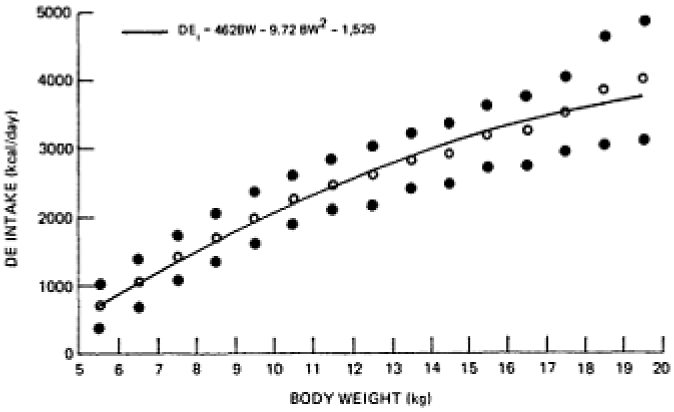

Figure 3-2
Digestible energy intake of pigs between 5 and 20 kg body weight. Mean values (°) and standard deviations (•) of 4,597 observations of 1,200 pens of pigs fed nutritionally adequate corn-soybean meal diets are shown (Ewan, 1983). Summaries were made at 1-kg increments.

Christianson et al., 1980), a model was developed for predicting swine performance. Maximum energy intake was defined as a quadratic function of body weight for weights from 10 to 45 kg and as a hyperbolic (arc sinh) function of weight in the range of 45 to 110 kg BW. Maximum energy intake was modified by effects of temperature. The derivations of the intake functions were, however, not documented in these reports.

Whittemore (1976) described a model of pig growth in which feed intake was described by an asymptotic relationship with body weight. Other relationships for feed intake were also presented that were linear functions of body weight, metabolic body weight, or days on feed. While Whittemore (1976) did not indicate a preferred function, all of the functions are limited if predictions are to be extended above or below the range in body weight of 20 to 100 kg.

ARC (1981) reviewed a number of reports of voluntary feed intake and used a large set of unpublished data of R.A. Houseman, I. McDonald, R. M. J. Crofts, and V. R. Fowler to derive relationships between body weight and feed intake. The observed relationship was

$$\mathrm{DE}_i = 1{,}123\mathrm{BW}^{0.51}. \qquad (5)$$

ARC also reported estimates of intake at 4 times maintenance by two equations:

$$\mathrm{DE}_i = 717\mathrm{BW}^{0.63} \qquad (6)$$

or

$$\mathrm{DE}_i = 13{,}145(1 - e^{-0.0204\mathrm{BW}}). \qquad (7)$$

No clear function for voluntary feed intake was defined, however, by ARC in that report.

In a model to simulate life cycle efficiency of pork production, Tess et al. (1983) estimated feed intake from the sum of the ME required for maintenance and that required for protein and fat deposition. Deposition of protein and fat were estimated from quadratic equations based on age.

Ewan (1983) summarized data from 62 experiments involving 8,072 observations of 1,490 pens of pigs fed nutritionally adequate corn-soybean meal diets. Pigs fed individually or pens of pigs were considered as experimental units, and observations of feed intake and body weight with time were summarized. The weight class means of pigs from 4.5 to 117 kg BW were fitted by nonlinear regression (Statistical Analysis System, 1982) to the asymptotic relationship, and the following equation was obtained (Figure 3-3):

$$\mathrm{DE}_i = 13{,}162(1 - e^{-0.0176\mathrm{BW}}). \qquad (8)$$

The standard error of the asymptote was 197 and that of the exponent was 0.0005. The equation is very similar to the relationship reported by ARC (1981). Data were not available to allow classification of the data set by environmental or physiological variables but should reflect the mean response over a wide variety of environmental conditions and physiological states.

The asymptotic relationship overestimates the DE_i of young pigs (Figure 3-3). The use of the quadratic relationship (Equation 2) described in the previous section on the weanling pig provides a better estimate of DE, by pigs in the weight range from 5 to 10 kg BW. From 10 to

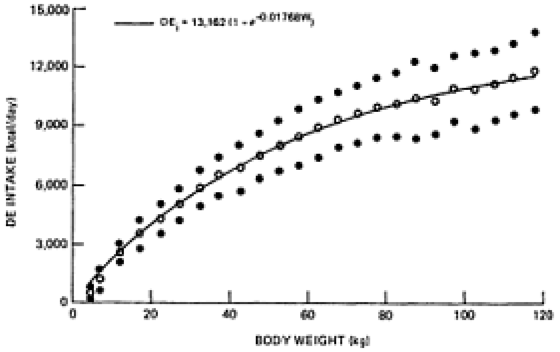

Figure 3-3
Digestible energy intake as an asymptotic function of BW. Mean values (°) and standard deviations (•) of 8,072 observations of 1,490 pens of pigs fed nutritionally adequate corn-soybean meal diets are shown (Ewan, 1983). Summaries were made at 5-kg increments.

20 kg BW, Equations 2 and 8 predict similar intakes. The asymptotic relationship should be restricted to use for pigs weighing more than 20 kg but could be used for pigs between 10 and 20 kg BW.

The basic equation form used to predict voluntary feed intake is dependent on the intake of the mature animal. Most of the data used to develop prediction equations for voluntary feed intake are in the range of data from 20 to 100 kg BW. The asymptotic relationship suggests that feed intake increases to a maximum level and is consistent with the concept of a maximum mature body size. ARC (1981) cites unpublished data of K. L. Blaxter and V. R. Fowler of the Rowerr Research Institute, Aberdeen, Scotland. Their data suggests that pigs fed ad libitum to maturity reach maximum intake at about 120 kg and that after 120 kg voluntary intake goes into unstable oscillation with a trend toward a slight decline. Data from experiments summarized by Ewan (1983) for pigs ranging in weight from 10 to 116 kg did not suggest a decline in daily intake at heavier weights and supported an asymptotic relationship. Lee and Bowman (1976) observed increasing feed intake by pigs weighing from 32 to 125 kg.

In contrast, Siebrits and Kemm (1982) observed a marked decline in daily feed intake above 70 kg BW by South African Landrace pigs. Daily feed intakes were, however, lower than those observed in other studies. Observations by Mahan and Gerber (1984) for 51 pens of pigs weighing from 56 to 150 kg indicated a slight decline in daily intake above 100 kg BW. The report of Giles et al. (1981) also supports a decline in daily intake above 60 kg BW. Friend (1973) reported a decline of 148 g of dry matter per week by gilts allowed ad libitum access to protein and cereal pellets. The body weight of the gilts increased from 125 to 180 kg during the 22-week period.

VOLUNTARY FEED INTAKE DURING GESTATION

Studies of energy requirements during gestation have indicated that restriction of energy intake results in better reproductive performance than when ad libitum consumption of energy is allowed (National Research Council [NRC], 1979). NRC (1979) recommended restriction of intake of bred gilts and sows to 1.8 kg of feed providing 6.12 Mcal of DE (5.76 Mcal of ME) daily. The NRC (1979) recommendations are considerably lower than the voluntary daily intakes of 12.6 to 18 Mcal of DE observed by Friend (1971) for bred gilts and sows. Voluntary intake of energy declined from mating to farrowing at a rate of 40.2 kcal/day for gilts and a rate of 47.8 kcal/day for sows (Friend, 1971). Sows consumed 13.8 percent more energy postweaning than gilts.

VOLUNTARY FEED INTAKE DURING LACTATION

During lactation the sow physiologically requires nutrients to support maintenance and milk production. Milk production has a high priority, and if nutrient intake is restricted, the sow will draw on body tissue in an attempt to maintain milk production. Provided with voluntary access to feed containing an adequate supply of nutrients, the sow will consume sufficient quantities of nutrients to maintain body weight and to support milk production.

Feed intakes during lactation reported in several studies are summarized in Table 3-3. In studies that reported data for gilts, average feed intake was 4.36 kg providing 14,430 kcal of DE daily. Feed intakes reported for sows (two or more parities) averaged 5.17 kg and provided 17,030 kcal of DE daily. Gilts consumed 15 percent less energy during lactation than sows. There is wide variation in the observed daily intakes of DE, from 11,452 to 21,689 kcal/day. This variability reflects a multitude of factors that can influence lactation feed intake.

Lactation feed intake is low immediately postfarrowing and increases as lactation proceeds. Most investigators have only reported lactation feed intake over the entire lactation period. O'Grady and Lynch (1978) and Stahly et al. (1981b) have reported weekly feed intake, and Stahly et al. (1976) reported daily intakes for the first 8 days of lactation and weekly values thereafter. With the data from these reports, the change in feed intake with time after farrowing was estimated to be

$$\mathrm{DE}_i = 13{,}400 + 596\mathrm{Day} - 17.2\mathrm{Day}^2, \qquad (9)$$

where DE_i is in kcal/day and Day is the day of lactation (Figure 3-4). The values for the standard error of the estimate of the linear coefficient, the quadratic coefficient, and the intercept were 149, 7.0, and 740, respectively. The relationship is valid for a lactation period of 28 days or less because the maximum lactation length in the data used was 28 days. The quadratic relationship predicts maximum intake on about day 17 of lactation, with a maximum intake of 18,440 kcal of DE daily. This relationship predicts an average intake of 17,200 kcal/ day for 26 days of lactation and compares favorably with the mean response for sows of 17,030 kcal daily reported in Table 3-3.

FACTORS AFFECTING VOLUNTARY FEED INTAKE

Physiological Factors

Part of the variability associated with feed intake can be attributed to differences in the genetic base or be tween breeds. Table 3-4 compares experiments in which feed intake for various breeds could be compared. Within experiments, the pigs of each breed had similar initial and final weights. Duroc and crossbred pigs tended to consume more feed than other breeds. Differences in daily voluntary intake probably occur between selected lines within breeds and between different crosses between lines. There are, however, insufficient data to allow quantitation of the effect of these variables on voluntary feed intake.

TABLE 3-3 Lactation Digestible Energy Intake

Study Reference	Average No. of Litters	No. of Pigs Weaned	Length of Lactation (days)	Daily intake	
				kg	kcal of DE
Gilts					
Baker et al., 1969	224	6.16	21	4.03	12,890
Elsley et al., 1969	132	8.20	56	5.61	20,859
Buitrago et al., 1974	71	6.97	56	3.69	11,797
Michel et al., 1980	161	8.20	28	4.26	13,640
Mahan and Fetter, 1982	23	7.10	28	4.80	15,360
Corley et al., 1983	133	7.14	28	3.76	12,035
Total	744				
Average		7.30	36.2	4.36	14,430
Maximum		8.20	56	5.61	20,859
Minimum		6.16	21	3.69	11,797
Standard deviation		0.79	15.6	0.73	3,402
Sows					
Jensen, 1964	17	8.33	28	4.30	13.771
Frobish et al., 1966	141[a]	8.23	14	3.85	12,328
Holden et al., 1968	235[a]	7.48	14	5.48	18,068
Elsley et al., 1969	220	8.80	56	5.83	21,689
Libal and Wahlstrom, 1975	62	8.20	21	6.46	19,759
Stahly et al., 1976	468	7.60	21	5.61	17,456
Haught et al., 1977	154[a]	8.10	35	5.79	18,536
Boyd et al., 1978	74[a]	6.60	14	4.63	16,434
O'Grady and Lynch, 1978	320	8.80	28	5.00	15,767
Michel et al., 1980	93	8.90	28	5.12	16,378
Pollmann et al., 1981	230	8.47	21	5.05	17,135
Pond et al., 1981	88	7.30	28	3.58	11,452
Seerley et al., 1981	96[a]	8.93	21	5.12	16,857
Stahly et al., 1981b	204	8.75	21	5.51	18,750
Boyd et al., 1982	188[a]	8.50	21	5.46	19,492
Mahan and Fetter, 1982	48	8.50	28	6.60	21,120
Yoo and Hann, 1982d	50	8.95	28	5.22	17,783
Corley et al., 1983	79	7.58	28	4.48	13,773
Total	2,767				
Average		8.22	25.2	5.17	17,030
Maximum		8.95	56	6.60	21,689
Minimum		6.60	14	3.58	11,452
Standard deviation		0.66	9.6	0.80	2,827

[a] These studies include data from gilts but do not report results for gilts and sows separately.

Voluntary feed intake by barrows is greater than the feed intake by gilts. Table 3-5 summarizes comparisons of feed intake between barrows and gilts and indicates that barrows consume 4.9 percent more feed than the average consumption of both barrows and gilts and that gilts consume 4.9 percent less feed than the average. Boars also tend to consume less feed than barrows. From the data reported by Siers (1975), Henry (1969), and Fowler et al. (1981), boars consumed 5.16 percent less feed than barrows.

The difference in feed intake by gilts and barrows is dependent on weight and is not observed during the starter, or postweaning, period. Data reported by Cop and Buiting (1977) compared intake of gilts and barrows at 5-kg increments from 25 to 95 kg and can be expressed by the following quadratic relationship:

$$\text{Percent deviation} = 0.2142\text{BW} - 0.00133\text{BW}^2 - 4.42, \quad (10)$$

where percent deviation indicates the change from the mean of barrows and gilts ($r^2 = 0.994$). The values for the standard error of the estimate of the linear coefficient, the quadratic coefficient, and the intercept were 0.0081, 0.00007, and 0.225, respectively. This relationship predicts that positive deviations begin at about 25 kg BW, increase to a maximum of 4.2 percent at 80 kg BW, and decline slightly thereafter. Similar responses have been reported by Tjong-A-Hung et al. (1972), Siers (1975), and Christian et al. (1980). Lee and Bowman (1976) reported a larger difference between barrows and gilts at 48 kg BW than would be predicted by Equation 10 and that the difference declined continuously to 136 kg BW.

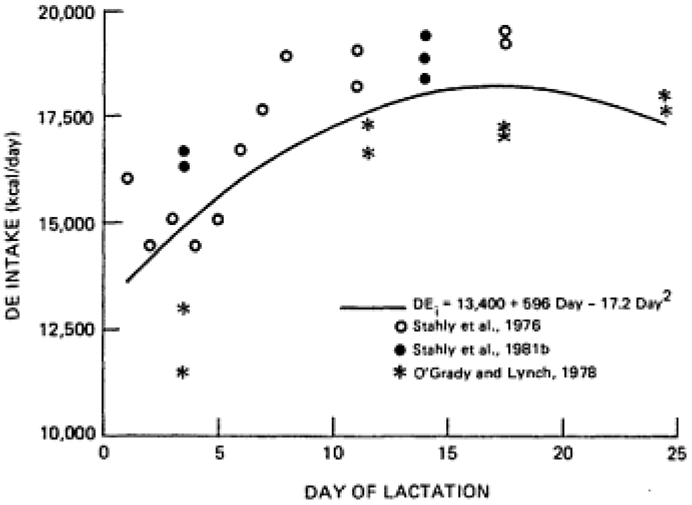

Figure 3-4

Digestible energy intake by lactating sows.

Friend (1973) reported that the voluntary intake of gilts during estrus decreased to 84.5 percent of the intake observed between estrus periods, indicating that the physiological state of the animal affects feed consumption. Lactating sows fed iodinated casein produce milk containing higher dry matter, protein, and energy than control sows (Aherne and Speer, 1974). Feed intake by sows fed iodinated casein was not affected or tended to decrease (Dudley et al., 1959).

Environmental Factors

Temperature is probably the most significant component of the environment that affects feed intake. NRC (1981) summarized much of the data related to the effects of environment on nutrient requirements. NRC (1981) indicates that there is a zone of thermoneutrality in which heat production is relatively stable. Upper and lower critical temperatures are defined as the upper and lower environmental temperatures where energy must be expended to heat or cool the body. The implication is that between the upper and lower critical temperatures, energy is not required to maintain body temperature

TABLE 3-4 Effect of Breed on Daily Digestible Energy Intake

Study Reference	Mean DE Intake (kcal/day)	Duroc	Hamp	York	PC	SPC	L	Cross
Johnson et al., 1973	7,104	6.7	0.0	-6.3				5.6
Quijandria et al., 1970	7,264	0.8	-0.8	2.9	1.7	-3.3		
Bruner and Swiger, 1968	7,971	1.6	-3.6	-1.2	-3.3	1.6	2.0	
Hale and Southwell, 1967	7,270	2.9	-3.1					
Bereskin et al., 1976	7,296	3.5		-3.5				
Bereskin et al., 1975	7,184	3.8		-3.8				
McPhee et al., 1979	6,352			1.8			-1.8	

NOTE: Values are the deviations from the mean, in percent. Hamp is Hampshire; York, Yorkshire; PC, Poland China; SPC, Spotted Poland China; L, Landrace; Cross, crossbreed.

and that feed intake is relatively stable. The zone of thermoneutrality is small for the newborn pig and increases with maturity.

TABLE 3-5 Effect of Sex on Daily Digestible Energy Intake

Study Reference	Weight Range (kg)	No.	Mean (kcal of DE/day)	% Deviation[a]
Clawson et al., 1962	17-90	72	8,544	2.2
Cole et al., 1967b	45-91	20	7,500	5.7
Hale and Southwell, 1967	20-96	60	7,270	5.0
Cole et al., 1968	59-91	64	10,216	4.6
Bruner and Swiger, 1968	20-94	1,452	7,971	5.5
Quijandria et al., 1970	20-91	1,632	7,264	4.0
Wahlstrom et al., 1971	18-96	112	7,840	3.3
Wahlstrom et al., 1971	16-96	112	7,827	5.4
Bereskin et al., 1975	18-101	128	7,168	3.7
Bereskin et al., 1976	20-100	96	7,312	7.7
Baird, 1973	16-100	120	8,241	4.9
Jensen et al., 1973	25-100	144	6,736	5.5
Fowler et al., 1981	30-90	86	8,620	5.5
Mahan and Gerber, 1984	59-135	360	9,107	5.7
Average			7,973	4.91

[a] Percent deviation is the percent change from the mean intake of barrows and gilts. Deviations are positive for barrows and negative for gilts. For example, in the study of Clawson et al. (1962), barrows in the 17-90-kg weight range ate 2.2 percent more digestible energy than average; the corresponding gilts ate 2.2 percent less. In this case, there is a 4.4 percent difference in digestible energy between the sexes.

Heitman et al. (1958) reported that weight gain was maximized at 23°C for 45-kg pigs and at 16°C for 159-kg pigs, with a linear response between these two weights. Heitman and Hughes (1949) reported that feed-to-gain ratios were minimized at the same temperatures that gave maximum gain. Verstegen et al. (1978) summarized the results of 34 studies on the effects of temperature on feed intake, rate of gain, and feed-to-gain ratio of growing-finishing pigs. They concluded that feed intake declined at a relatively uniform rate as temperature increased from 5 to 20°C. Between 20 and 25°C the rate of feed intake decline was less than the rate of decline from 5 to 20°C. The temperature range can be extended to 30°C by including data for growing-finishing pigs reported by Nichols et al. (1980), Heitman and Hughes (1949), and Close and Mount (1976, 1978) and data for weanling pigs reported by Le Dividich et al. (1977). With intake at 15°C established as 100, intake declined linearly from 5 to 30°C by the following relationship:

$$\text{Percent change} = 126.3 - 1.65T, \qquad (11)$$

where percent change reflects the deviation from feed intake at 15°C, and T is the reported ambient temperature in °C (Figure 3-5). The values for the standard error of the estimate of the regression coefficient and the intercept were 0.14 and 2.85, respectively ($r^2 = 0.826$).

Data reported by Nichols et al. (1980) suggest that extreme cold stress drastically increases voluntary feed intake. Intake at 5°C was 119 percent of the intake at 15°C but intake at 0°C was 161 percent of intake at 15°C.

Extreme heat stress drastically decreases feed intake. Expressed as a percentage of intake at 15°C, Heitman and Hughes (1949) observed intakes of 43.3 percent at 37°C and 21.7 percent at 46°C by pigs weighing between 31 and 65 kg. Nichols et al. (1980) reported that intake at 35°C was 48.1 percent of the intake at 15°C.

Temperature stress has a greater effect on heavy (70 to 118 kg) pigs than on light (40 to 70 kg) pigs. Verstegen et al. (1978) reported greater depressions of growth rate for heavy pigs than for light pigs with heat or cold stress. Heitman and Hughes (1949) reported that at 37°C pigs weighing between 75 and 118 kg reduced feed intake about 60 percent more than pigs weighing between 31 and 65 kg.

The temperature of the environment is modified by several physical factors, and the term effective ambient temperature (EAT) has been used to describe the temperature that the animal experiences (NRC, 1981; Curtis, 1983). This adjusted temperature could be used to correct feed intake for deviations from the optimal temperature.

The moisture content of the air and the temperature of the environment interact to influence feed intake and performance of pigs. During heat stress the pig depends on evaporative heat loss (panting) to lose heat. Feed intake is reduced and additional energy is required for heat loss and growth depression occurs. For swine the following relationship was suggested for adjusting ambient air temperature for humidity (Christianson et al., 1980; Curtis, 1983):

$$(0.65 \times \text{dry bulb temperature}) + (0.35 \times \text{wet bulb temperature}). \quad (12)$$

Air movement decreases the EAT by increasing the rates of convective and evaporative heat loss. Mount (1975) concluded that rates of air movement of 0, 0.2, 0.5, and 1.5 m/sec change EAT by 0, -4, -7, and -10°C, respectively. In addition, Mount (1975) suggested the following changes in EAT for various floor types: straw bedding, 4°C; concrete slats, -5°C; wet surface, -5 to -10°C. Curtis (1983) applied the variables estimated by Mount (1975) and further considered the insulative capacity of the walls of the building to estimate the EAT. Bruce and Clark (1979) evaluated the effects of live weight, feed intake, group size, and thermal environment on rate of heat loss and lower critical temperature. The resulting deterministic model provided valid estimates of heat production in the thermal neutral zone and below the critical temperature.

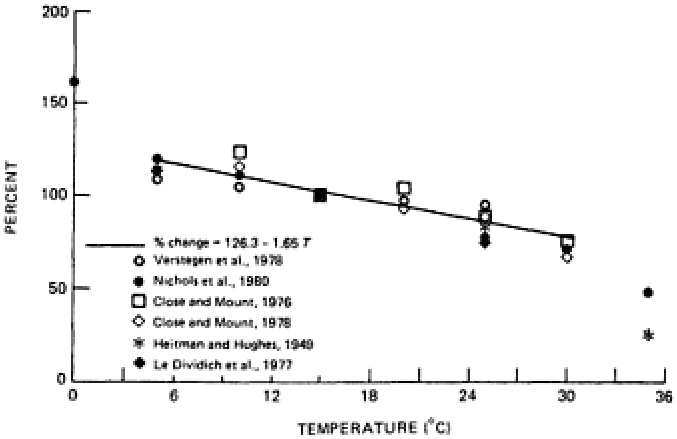

Figure 3-5
Effect of temperature on digestible energy intake.

From the data of Heitman et al. (1958), the optimal temperature (T_0) of 23°C for 45-kg pigs and 16°C for 159-kg pigs suggests the following relationship for the effect of body weight on optimal temperature:

$$T_o = 26 - 0.0614\text{BW}. \qquad (13)$$

Assuming that the deviation from the T_0 would affect feed intake, as suggested by Verstegen et al. (1978) and others, then:

$$\text{Percent change in DE}_i = (T_o - \text{EAT})0.0165. \qquad (14)$$

This correction would appear to be valid between 5 and 30°C, but greater changes in feed intake occur beyond this temperature range.

The number of pigs in a pen and the available space per pig both influence feed intake and performance of pigs. Increasing the number of pigs increases EAT by allowing the pigs to huddle in a cool environment and, therefore, reduce heat loss (Mount, 1975). In a warm environment, reduction of space allowance per pig is detrimental because body heat cannot be easily dissipated. Increasing the number of pigs per pen tends to increase the number of aggressive acts, and this effect is further increased if the space allowance per pig is reduced (Randolph et al., 1981).

With weanling pigs, Lindvall (1981) showed a 9 percent reduction in feed intake when space allowances were reduced from 0.25 to 0.17 m^2/pig and a further reduction of 10 percent if the space allowance was reduced from 0.17 to 0.13 m^2/pig. The North Central Region-89 Committee on Confinement Management of Swine (1984) reported a 7 percent reduction in feed intake if the space allowance was reduced from 0.23 to 0.14 m^2/pig. Similar observations for growing-finishing pigs indicate that below 1 m^2/pig, reduction in the space allowance results in 3 to 10 percent reduction in feed intake, with a tendency for a greater percent decrease as the restriction becomes more severe (Table 3-6).

Kornegay and Notter (1984) reviewed effects of space allowance on the performance of weanling (8 to 21 kg), growing (27 to 54 kg), and finishing (44 to 92 kg) pigs. They derived quadratic relationships between daily feed intake and space allowance within each weight group. By calculating the predicted feed intake and expressing feed intake as a percentage of the maximum predicted intake, the following relationships can be derived:

$$\text{Weanling, percent change} = 72.27 + 132.40S - 159.54S^2 \qquad (15a)$$

$$\text{Growing, percent change} = 77.25 + 42.93S - 20.25S^2 \qquad (15b)$$

$$\text{Finishing, percent change} = 61.65 + 70.05S - 32.00S^2 \qquad (15c)$$

where percent change is the deviation from optimal feed intake, and S is the space allowance in m^2.

Kornegay and Notter (1984) reported r^2 values of 0.97, 0.93, and 0.74 for the original prediction equations for weanling, growing, and finishing pigs, respectively. The space allowances for optimal feed intake were 0.4

m^2 for weanling, 1.06 m^2 for growing, and 1.09 m^2 for finishing pigs.

TABLE 3-6 Effect of Space Allocation on Daily Feed Intake

Study/Reference	Weight Range (kg)	Space Allowance (m^2/pig)		Feed Intake (kg)		
		High	Low	High	Low	% Change
Gehlbach et al., 1966	14-50	0.36	0.18	1.535	1.370	-10.7
Gehlbach et al., 1966	14-50	0.54	0.36	1.600	1.535	-4.1
Randolph et al., 1981	16-42	0.66	0.33	1.540	1.480	-3.9
NCR-89, 1986	35-57	0.46	0.32	1.830	1.770	-3.3
Handlin et al., 1972	35-56	1.06	0.79	2.200	2.040	-7.3
Handlin et al, 1972	35-56	1.28	1.06	2.150	2.200	2.3
Gehlbach et al., 1966	50-70	0.54	0.36	2.310	2.070	-10.4
Gehlbach et al., 1966	50-70	0.72	0.54	2.375	2.310	-2.7
Heitman et al., 1961	50-75	1.47	0.84	2.170	2.060	-5.1
Heitman et al., 1961	50-77	2.97	1.47	2.320	2.170	-6.5
Krider et al., 1975	50-100	0.63	0.43	2.610	2.170	-16.8
Gehlbach et al., 1966	70-90	0.72	0.54	2.715	2.520	-9.2
NCR-89, 1986	57-96	0.74	0.56	2.680	2.560	-4.5
Gehlbach et al., 1966	70-90	0.90	0.72	2.645	2.715	2.6
Handlin et al., 1972	57-91	1.06	0.79	3.030	2.850	-5.9
Handlin et al, 1972	57-91	1.28	1.06	2.930	3.030	3.4
Jensen et al., 1973	25-100	0.54	0.36	2.145	2.000	-6.7
Krider et al, 1975	28-98	0.63	0.43	2.410	2.240	-7.0
Krider et al., 1975	19-100	0.63	0.43	2.165	1.950	-9.9
Jensen et al, 1973	25-100	0.72	0.54	2.200	2.145	-2.5
Randolph et al., 1981	21-89	1.25	0.82	2.200	2.030	-7.7

Gehlbach et al. (1966) reported that with constant space allowance (0.36 m^2/pig) feed intake was 10 percent lower in pens containing 16 pigs as compared with pens containing 8 or 12 pigs during the growing period. During the finishing periods, pens containing 8 pigs consumed 6 percent less feed than pigs in pens containing 4 or 6 pigs with a constant space allowance (0.72 m^2/pig).

Kornegay and Notter (1984) also summarized the effects of varying the number of pigs per pen with a constant space allowance. With weanling pigs in a range of 3 to 15 pigs per pen, feed intake decreased 0.92 percent per additional pig in the pen ($r^2 = 0.97$). With growing pigs in a range of 5 to 32 pigs per pen, feed intake decreased 0.25 percent per additional pig in the pen ($r^2 = 0.87$). With finishing pigs in a range of 4 to 30 pigs per pen, feed intake increased 0.32 percent per additional pig in the pen ($r^2 = 0.92$).

While it is clear that both group size and space allowance influence the consumption of feed by growing pigs, quantitation of the response is not possible with the available data. Individually penned pigs have been reported to consume less feed than pigs fed in groups (Cole, 1967a), suggesting that there may be a desirable group size for maximizing feed intake and performance.

Nutritional Factors

The pig is generally considered to regulate feed intake to maintain a constant daily intake of energy. Therefore, the weight of feed that is consumed is determined by the energy density of the diet fed. As the energy density of the diet increases, the amount of feed consumed decreases to maintain constant energy intake. Assuming that the growth rate is maintained, the feed-to-gain ratio improves.

Pigs weaned at 14 to 21 days of age and fed diets varying in energy density have a limited ability to regulate intake based on energy density. Most studies with pigs of this age have involved an increase in the energy density by the addition of fat in an attempt to maintain a rapid growth rate during the postweaning period. Growth rate and feed-to-gain ratios, however, were not improved in many of these studies (Peo et al., 1957; Asplund et al., 1960; Sewell et al., 1961; Eusebio et al., 1965; Sewell and Miller, 1965; Frobish et al., 1969, 1970, 1971; Leibbrandt et al., 1975a,c; Menge and Frobish, 1976; O'Grady, 1978; Yoo and Han, 1982a; Lawrence and Maxwell, 1983). If pigs are weaned at greater than 21 days of age and allowed a period to recover from the stress of weaning, increasing energy density has been observed to improve feed efficiency (Sewell and Miller, 1965; Allee et al., 1971; O'Grady, 1978; Aherne et al., 1982a).

Among the studies that have reported DE intake in young pigs, Bowland (1964), Allee et al. (1971), and Wilson and Leibholz (1979) did not observe any significant effects of varying energy density on DE intake.

Leibbrandt et al. (1975a) observed an increase in DE intake as energy density increased. McConnell et al. (1982) observed a quadratic response in DE intake when the energy density was varied from 3,000 to 3,700 kcal/ kg, with maximum DE intake at 3,300 and 3,500 kcal/ kg.

Figure 3-6 summarizes the effect of varying the energy density for two weight groups of pigs. Studies with young pigs, with average weights of from 5 to 30 kg, indicate that daily DE intake is relatively stable with diets containing 3.3 to 3.6 kcal/g. With diet energy densities of less than 3.3 kcal/g, the young pig is unable to maintain daily DE intake, and daily DE intake decreases 1,388 kcal/day as energy density decreases 1 kcal/g. With diets containing more than 3.6 kcal/g, the young pig overconsumes energy, and DE intake increases at a rate of 183 kcal/day for an increase in energy density of 1 kcal/g. Pigs with average weights greater than 30 kg are also unable to maintain daily DE intake when energy density is less than 3.3 kcal/g. DE intake decreases 2,773 kcal/day for a decrease in energy density of 1 kcal/g. With diets containing 3.3 kcal/g and above, daily DE intake is relatively constant.

Deficiencies or excesses of nutrients in diets, in general, decrease feed intake. These changes require extremes in the dietary concentration of nutrients that are not generally encountered in practical diets. For example in growing pigs, protein levels of greater than 25 to 30 percent (Wagner et al., 1963; Sugahara et al., 1969) or less than 10 to 12 percent (Robinson et al., 1974) result in significant decreases in DE intake, but levels between these extremes have little effect on DE intake (Catron et al., 1952; Jensen et al., 1955; Gilster and Wahlstrom, 1973; Kornegay et al., 1973). In contrast, deficiencies of certain amino acids can depress feed intake rapidly and severely (Robinson, 1975; Montgomery et al., 1978).

Antibiotics have been used in swine diets for growth promotion for many years. Hays (1979) summarized the existing research reports of the effects of antibiotics on growth rate and feed efficiency. Stimulation of feed intake can explain a portion of the response to antibiotics. During the starter phase, pigs fed antibiotics consumed 8 percent more feed than controls. During the growing phase, the response was reduced to 6 percent more than controls, and during the finishing phase, intake was only slightly improved (2 percent) in pigs fed antibiotics.

Flavors have been reported to stimulate feed intake by weanling pigs (Campbell, 1976; King, 1979). Preference tests have indicated that weanling pigs do have preferences for specific flavors (McLaughlin et al., 1983). When no choice is given, however, feed intake is not stimulated by a variety of flavors (Kornegay et al., 1979; Ogunbameru et al., 1979; McLaughlin et al., 1983).

Pelleting of feed has resulted in varied responses in feed intake. VanChoubroek et al. (1971) reviewed the effect of pelleting of feed on pig growth rate, feed intake, and feed efficiency. From the results of 13 trials, they concluded that pelleting resulted in a 9.0 percent reduction in feed intake in weaned pigs. They summarized results from 79 trials with finishing pigs and concluded that there was a 3.1 percent reduction in feed intake if the feed was pelleted. A portion of the reduc

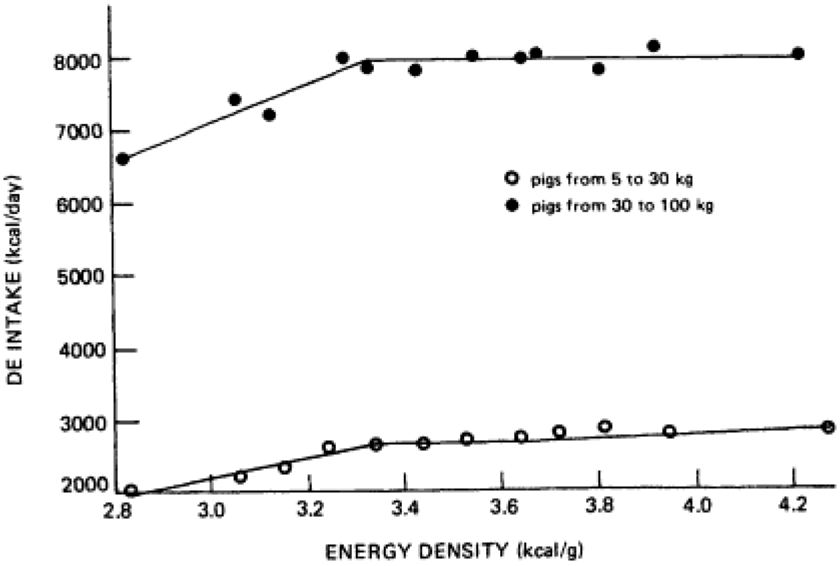

Figure 3-6
Effect of energy density on daily DE intake. Data from the following reports were used to derive the figure: Aherne et al., 1982a; Allee et al., 1971; Armstrong and Clawson, 1980; Asplund et al., 1960; Baird et al., 1970, 1975; Bowland, 1964; Campbell, 1977; Clawson, 1967; Corley et al., 1978; Eusebio et al., 1965; Frank et al.,1983; Frobish et al., 1969, 1970, 1971; Gilster and Wahlstrom, 1973; Henry, 1969; Hines, 1980a,b; Kass et al., 1980; Keaschall et al., 1983; Kornegay, 1978; Lawrence and Maxwell, 1983; Leibbrandt et al., 1975a,c; Lindemann et al., 1983; McConnell et al, 1982; Menge and Frobish, 1976; Mitchell et al., 1965; Moser et al., 1982; Nobler et al., 1980; Noland and Scott, 1960; O'Grady, 1978; Peo et al., 1957; Pond et al., 1962; Rodriguez et al., 1982; Seerley et al., 1978; Sewell and Miller, 1965; Sewell et al., 1961; Sherry et al., 1981; Stahly and Cromwell, 1979; Stahly et al., 1981a; Tribble et al., 1979; Wilson and Liebholz, 1979; Yoo and Han, 1982a,b,c.

tion in feed intake was attributed to a reduction in feed wastage, but this effect was difficult to measure accurately.

PREDICTING VOLUNTARY FEED INTAKE

Daily voluntary feed intake of growing pigs can be predicted by estimating DE consumption under thermo-neutral conditions. The estimated consumption can then be adjusted for physiological, environmental, and nutritional factors. The basic prediction relationships for various weight classes are as follows. For body weights from 5 to 20 kg:

$$\mathrm{DE}_i = 462\mathrm{BW} - 9.72\mathrm{BW}^2 - 1{,}529. \qquad (2)$$

If weaning stress is considered with weaning at 21 days of age, intake postweaning would increase from 0 at weaning at a rate of 100 kcal/day until intake equals the DE_i predicted from the quadratic relationship. For body weights from 10 to 120 kg:

$$\mathrm{DE}_i = 13{,}162(1 - e^{-0.0176\mathrm{BW}}). \qquad (8)$$

For growing pigs the following adjustment factors can be used. For pigs above 25 kg, adjustments can be made for deviations from equal numbers of barrows and gilts. The deviation in intake can be calculated from the following relationship:

$$\text{Percent deviation} = 0.2142\mathrm{BW} - 0.00133\mathrm{BW}^2 - 4.42. \qquad (10)$$

The percent deviation would be subtracted for gilts and added for barrows. Similar deviations can be used for boars and would be subtracted.

The adjustment for temperature requires calculation of the EAT, as described by Curtis (1983) or Bruce and Clark (1979), and the T_0 from the following relationship:

$$T_o = 26 - 0.0614\mathrm{BW}. \qquad (13)$$

Within the EAT range of 5 to 30°C, adjustment for temperature would be as follows:

$$\text{Percent change} = 0.0165(T_o - \mathrm{EAT}). \qquad (14)$$

The adjustment factors for inclusion of antibiotics would be 8 percent from weaning to 16 kg, 6 percent from 16 to 57 kg, and 2 percent from 57 kg to market weight. Adjustment for pelleting would be -9 percent from weaning to 20 kg and -3.1 percent from 20 kg to market. Adjustments for energy density for pigs from weaning to 30 kg are to decrease energy intake by 1,388 kcal/day for each kcal decrease below 3.3 kcal/g, no adjustment between 3.3 and 3.6 kcal/g, and for each kcal above 3.6 kcal/g an increase of 183 kcal/day. For pigs from 30 kg to market, DE, is decreased 2,773 kcal/ day for each kcal/g decrease below 3.3 kcal/g; above 3.3 kcal/g no adjustment is necessary.

The adjustment for allowance for various weight groups would be as follows:

$$\text{Weanling (5–20 kg) percent change} = 72.27 + 132.40S - 159.54S^2 \qquad (15a)$$

$$\text{Growing (20–50 kg), percent change} = 77.25 + 42.93S - 20.25S^2 \qquad (15b)$$

$$\text{Finishing (50–100 kg), percent change} = 61.65 + 70.0S - 32.00S^2 \qquad (15c)$$

The adjustment for the number of pigs per pen would be -0.92 percent per pig for weanling pigs, -0.25 percent per pig for growing pigs, and 0.32 percent per pig for finishing pigs.

For lactating sows during a lactation period of 28 days or less, DE_i can be estimated from the following relationship:

$$\mathrm{DE}_i = 13{,}400 + 596\mathrm{Day} - 17.2\mathrm{Day}^2 \qquad (9)$$

The predicted DE intake can be adjusted for temperature as described above for growing pigs.

EXAMPLE PREDICTIONS

A pelleted diet containing 3.3 kcal of DE/g and antibiotics is fed to a 5-kg pig in an environment with an EAT of 25°C.

Predicted intake: $\mathrm{DE}_i = 462(5) - 9.72\,(5^2) - 1{,}529 = 538$ kcal/day

Temperature adjustment: $T_o = 26 - 0.0614(5) = 25.7$ $(538)[0.0165(25.7 - 25)] = 6$ kcal/day

Antibiotic adjustment: $(538)(0.08) = 43$ kcal/day

Pelleting adjustment: $(538)(-0.09) = -48$ kcal/day

Net intake: $538 + 6 + 43 - 48 = 539$ kcal/day

A diet containing 3.0 kcal of DE/g is fed to a 50-kg barrow in an environment with an EAT of 15°C.

Predicted intake: $\mathrm{DE}_i = 13{,}162(1 - e^{-0.0176(50)}) = 7{,}702$ kcal/day

Sex adjustment: $\text{Percent deviation} = 0.2142(50) - 0.00133(50)^2 - 4.42 = 2.965$ $(7{,}702)(0.02965) = 228$ $7{,}702 + 228 = 7{,}930$

Temperature adjustment: $T_o = 26 - 0.0614(50) = 22.9$ $(7{,}930)[0.0165(22.9 - 15)] = 1{,}034$ kcal/day

Energy density adjustment: $(3.3 - 3.0)(-2{,}773) = -832$

Net intake: $7{,}702 + 228 + 1{,}034 - 832 = 8{,}132$ kcal/day

A diet containing 3.3 kcal of DE/g is fed to a pen containing 6 gilts and 14 barrows weighing 70 kg and in an environment with an EAT of 15°C.

Predicted intake: $DE_i = 13{,}162(1 - e^{(-0.0176)(70)}) = 9{,}323$ kcal/day

Adjustment for sex: Percent deviation $= 0.2142(70) - 0.00133(70^2) - 4.42 = 4.057$

$9{,}323(0.04057) = 378$ kcal/day

DE_i of barrows $= 9{,}323 + 378 = 9{,}701$

DE_i of gilts $= 9{,}323 - 378 = 8{,}945$

Pen De_i: $0.7(9{,}701) + 0.3(8{,}945) = 9{,}474$

Adjustment for number of pigs for pen: $20(0.0032) = 0.064$

$(9{,}474)(0.064) = 606$

Adjustment for temperature: $T_c = 26 - 0.0614(70) = 21.7$

$9{,}474[0.0165\,(21.7 - 15)] = 1{,}047$

Net average intake: $9{,}474 + 606 + 1{,}047 = 11{,}127$ kcal/day

A 200-kg sow on day 7 of lactation is fed a diet containing 3.3 kcal/g in an environment with an EAT of 25°C.

Predicted intake: $DE_i = 13{,}400 + 596(7) - 17.2(7^2) = 16{,}729$

Temperature adjustment: $T_c = 26 - 0.0614(200) = 13.7$

$16{,}729\,[0.0165(13.7 - 25)] = -3{,}119$

Net intake: $16{,}729 - 3{,}119 = 13{,}610$

Validation

While attempts have been made in this chapter to quantitate a number of variables that affect the voluntary intake of pigs, it should be recognized that additional factors influence voluntary feed intake. In attempts to validate the relationships proposed in this chapter, data that were obtained from experiments not used to develop the relationships were used. Predicted intakes were calculated from initial body weight and growth rate on a daily basis by pen and adjusted for factors for which information was available. Data reported by Nienaber (1981) were available and involved variables of energy density and temperature for pigs weighing from 5 to 30 kg. Intake was overpredicted by 16 percent and may have been because the pigs were maintained in calorimeters during a portion of the studies. Actual measured energy values were used for the feeds and may have been lower than the actual values. There was no indication of systematic errors in the predicted values. Data from studies reported by Kinyamu (1985) for pigs (5-20 kg BW) fed diets varying in energy density were also compared to predicted intake. Predicted intakes were 91 and 96 percent of actual values, and no systematic pattern was apparent in the differences between actual and predicted values. Data reported by Mahan and Gerber (1984) were also compared to predicted values. The pigs in this study were fed from 60 to 136 kg (beyond the range of the data used to develop the basic equation), and the predicted values were 22 percent greater than actual intakes for gilts and 15 percent greater for barrows. Mahan and Gerber (1984) observed a decline in daily intake at heavier weights, and this decline did not occur with the proposed relationship.

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4

Poultry

INTRODUCTION

With the exception of meat-type broiler breeders and a few strains of egg-laying hens, feeding systems for poultry are usually based on ad libitum feeding. The producer determines the nature and quality of the feed, but the bird itself governs feed intake. The birds are usually maintained in a controlled environment with regard to temperature and airflow, although systems differ in complexity and the degree of control that is attainable.

FEED INTAKE CONTROL MECHANISMS

There is considerable disagreement about the mechanisms that control feed intake in poultry. (See Chapter 1 for an overall view of feed intake control mechanisms in animals.) In poultry, dietary energy, protein, weight, and volume all have significant effects upon feed consumption (reviewed by Gleaves et al., 1968). Both peripheral and central neural controls have been implicated in the regulation of feed intake. Peripheral receptors in the upper digestive tract serve as important regulators of feed intake and are presumed to be interrelated and in contact with the hypothalamus via neurons (Polin and Wolford, 1973). At least five theories, each based upon a variable monitored by the central nervous system, have been advanced to explain the control of feeding. These include the glucostatic, thermostatic, lipostatic, aminostatic, and ionostatic theories.

Glucostatic Theory

The glucostatic theory of feed intake regulation, as generally recognized in mammals, either is not present in birds or is not readily detectable by normal protocols (Richardson, 1970; Smith and Bright-Taylor, 1974). Food intake has not been augmented as it has in mammals after the implantation of gold thioglucose directly into several hypothalamic structures (Smith and Szper, 1976) or after peripheral injections (Gentle, 1976; Walker et al., 1981). Feeding has not been altered after manipulation of blood glucose levels (Smith and Bright-Taylor, 1974). More recent studies have suggested possible roles of central (Denbow et al., 1982) and peripheral (Shurlock and Forbes, 1981) glucoreceptors in affecting feed intake. However, when the glucose analog 2-deoxy-D-glucose (an inhibitor of glycolysis that causes a depression of intracellular glucose utilization) was injected intraperitoneally into fowl, it did not effect an increase in food intake (Smith et al, 1975). Hence, the importance of blood glucose or a change in blood glucose in controlling feed intake in chickens is unresolved at this time.

Thermostatic Theory

The thermostatic theory is based upon the output (loss) of body heat or energy that drives a bird to conserve body heat and/or consume food. It requires a central controller (presumably in the brain) and several peripheral detectors to sense temperature changes. Progress has been made in poultry and other avian species to demonstrate that an anterior hypothalamic area contains thermally sensitive loci for induction of thermoregulatory responses (Mills and Heath, 1970). Thermoreceptors have been identified in the bill (Necker, 1973), skin (Necker, 1977), and spinal cord (Rautenberg et al., 1972). The relationships between environmental temperature and feed intake and between temperature and heat production are reasonably well known in birds (Calder and King, 1974; Sykes, 1979). However, more data are needed to determine if a thermostatic mechanism is a primary controller of feed intake.

Lipostatic Theory

The lipostatic theory is based upon feedback from fat depots to the brain for long-term regulation of feed intake. Based upon studies using the technique of forced feeding, Lepkovsky (1973) has suggested that a lipostatic mechanism for the control of feed intake regulation exists in poultry. The studies of Polin and Wolford (1973) have indicated that lipostatic systems show evidence of influence on feed intake, but the effects are not totally consistent with the proper functioning of a lipostatic mechanism. A recent study in which partial lipectomy was performed in both Leghorn and broiler chicks showed no compensatory feed intake response in either type of bird. The data suggest little, if any, negative feedback from adipose tissue mass in chickens (Maurice et al., 1983).

Aminostatic Theory

It has been known for years that the balance of amino acids markedly influences food intake in both chicks and rats. Imbalanced diets cause rapid decreases in food intake and altered patterns of feeding (Rogers and Leung, 1973). The addition of single amino acids or groups of amino acids to the diet depresses growth rate (Fisher and Shapiro, 1961; Harper et al., 1970). Force feeding prevents the typical growth depression due to amino acid imbalance in chicks (Austic and Scott, 1975), indicating that the negative consequences of imbalance are due, ultimately, to reduced feed intake. The consumption of imbalanced diets leads to a rapid decrease in the concentration of the first limiting amino acid in the blood (Harper et al., 1970). This may be the signal that triggers a reduction in appetite. Data suggest that the brain contains receptors for amino acids or their metabolites. In studies by Tobin and Boorman (1979) young cockerels were fed a low-protein diet, imbalanced by the addition of an essential amino acid mixture lacking histidine. Infusion of histidine via the carotid artery significantly increased food intake, whereas infusion via the jugular vein did not. Thus, infusion via the carotid artery rectifies the pattern of amino acids passing to the brain, causing the cockerel to respond as if the dietary amino acid pattern were balanced. Specific brain loci appear to be involved in giving mammals the ability to detect an amino acid-imbalanced diet (Leung and Rogers, 1971). Since comparable brain areas have not been discovered in poultry to date, the aminostatic theory and the mechanism responsible for monitoring changes in the protein concentration of the diet remain the subject of speculation.

Ionostatic Theory

The extracellular role of Na^+ and Ca^{++} ions within the brain (more specifically the hypothalamus) has marked effects upon body temperature and feed intake. The set point for body temperature in mammals was proposed to be controlled by the ratio of Na^+ and Ca^{++} ions. An excess of the latter caused hypothermia (Myers and Veale, 1970). Further studies showed that an elevated concentration of brain calcium induced feeding in satiated rats (Myers et al., 1972). To date, the ionostatic theory has not been adequately studied in poultry.

Role of Brain Structure

The theories presented above have all implied that specific brain structures are involved in the control of feed intake. A few brain loci have been identified that have clear effects on feed intake or body composition in poultry. Obesity without hyperphagia has been effected in the chicken after placement of large lesions within the medial basal hypothalamic region (Lepkovsky and Yasuda, 1966). In no paper published to date has it been shown clearly which neural structures need to be destroyed to illicit hyperphagia and obesity in poultry. It was surmised that the ventromedial hypothalamic nucleus is a critical neural substrate (Kuenzel, 1974). However, lesions were large and obviously encroached upon other structures such as the inferior hypothalamic nucleus, medial mammillary nucleus, ventral noradrenergic bundle, dorsomedial hypothalamic nucleus, and periventricular hypothalamic nucleus.

Transient aphagia or hypophagia has been produced in chickens (Feldman et al., 1957), broiler chickens (Kuenzel, 1982), and other avian species following bilateral lesions in and around the lateral hypothalamic-thalamic and midbrain areas. Structures that appear to be the most important for effecting aphagia/hypophagia in various avian species are the following: ansa lenticularis, posterior nucleus of the ansa lenticularis, and quinto-frontal tract (Kuenzel, 1982); stratum cellulare externum and lateral forebrain bundle (Wright, 1975); and quinto-frontal tract and trigeminal structures (Ziegler and Karten, 1973).

Summary

In summary, it is unclear at this time which of the five proposed theories of feed intake best applies to poultry. It is also unclear which brain structures are important in regulating feed and water intake. Biologists have not yet identified with assurance either the site or the nature of a mechanism which specifically regulates food intake in birds. A number of excellent reviews have been written on factors regulating feed intake in poultry (Gleaves et al., 1968; Polin and Wolford, 1973; Boorman and Freeman, 1979), and interested readers are directed to these reviews.

It is generally recognized among poultry nutritionists that a primary determinant of feed intake is the energy concentration of the diet. These studies have been reviewed in detail by Waldroup et al. (1976), Pesti (1982), and Pesti and Fletcher (1983). As the level of metabolizable energy in the diet increases or decreases, food intake changes inversely, although the rate of adjustment is not always sufficient to keep energy intake constant. As the energy content of the diet increases, there is almost always a greater daily intake of calories by the bird (Morris, 1968).

Since poultry are generally offered diets containing low-moisture ingredients such as cereal grains and animal or vegetable protein supplements, there has been little emphasis upon estimating dry matter intake in this species. Rather, the emphasis has been upon estimating either total feed intake, by assuming a constant dietary energy, or upon estimating an energy requirement, thus allowing for an estimation of feed intake from knowledge of the dietary energy content. As more studies are conducted on the estimation of true metabolizable energy, amino acid digestion, and carcass retention of nutrients, more emphasis likely will be given to dry matter intake.

ESTIMATING FEED INTAKE OF LAYING HENS

Laying hens attain a virtual steady state of feed consumption once peak production has been attained, thus allowing for more consistent estimates of feed intake as influenced by various production and environmental factors. Nutrient requirements of laying hens are increasingly being expressed on a daily intake basis, thus implying the importance of knowledge of daily intake of total feed. Because of this, a greater emphasis has been placed upon estimating feed intake in laying hens than in other poultry species.

Byerly (1941) reported an equation for estimating the daily feed intake of laying hens varying in body weight from about 1 to 3 kg. The 0.653 power of body weight gave the best estimate of feed requirement for maintenance from these data. This equation was later modified by Combs (1968) to express the nutrient needs in terms of apparent metabolizable energy (AME) adjustable to various ambient temperatures.

Byerly et al. (1980) have developed partition equations that describe the feed intake for five genetically different groups of hens, including small Leghorns, white egg hybrids, brown egg hybrids, female line broiler breeders, and broiler-cross pullets. For the first four groups, equations that assume a 70 percent efficiency of use of metabolizable energy (ME) for maintenance, tissue formation, and egg formation gave the best fit to the observed data. The equations were as follows:

$$F = (0.534 - 0.004T)W^{0.653} + 2.76\Delta W + 0.80\mathrm{EM} \qquad (1)$$

and

$$F = (0.259 - 0.00259T)W^{0.75} + 2.76\Delta W + 0.80\mathrm{EM} \qquad (2)$$

where F is feed/hen/day (g), T is ambient temperature (°C), W is live weight (g), W is daily change in live weight (g), and EM is egg mass/hen/day (g).

For broiler-cross pullets, an energetic efficiency of 65 percent gave the best fit to the data. Corresponding equations for this type of pullet were as follows:

$$F = (0.589 - 0.0044T)W^{0.75} + 2.9\Delta W + 0.85\mathrm{EM} \qquad (3)$$

$$F = (0.275 - 0.00275T)W^{0.75} + 2.9\Delta W + 0.85\mathrm{EM}. \qquad (4)$$

These equations were developed using the diets containing 2,890 kcal of AME/kg. Morris (1968) observed an effect of dietary energy level on voluntary feed consumption, and Byerly et al. (1980) noted that this effect should be considered when dietary energy levels differ markedly from 2,890 kcal of AME/kg. Morris (1968) analyzed the data from 34 published reports and observed that groups of hens offered diets with different energy levels tend to adjust consumption so as to maintain a similar caloric intake; however, the adjustment is imperfect in the majority of cases. This is especially true when high-energy diets containing supplemental fats are fed to hens. Under such circumstances hens tend to overconsume calories. This does not necessarily result in higher egg production; hens fed such diets usually have slightly larger eggs and usually show increased body weight gains that reflect greater stores of adipose tissue and not protein (muscle tissue).

Morris (1968) noted that the degree of energy over-consumption observed when a particular strain of hen is offered a range of diets, each with a different energy content, is correlated with the characteristic caloric intake of that strain. Strains with characteristically high caloric intakes adjust their food consumption to compensate for differences in energy content of the diet less efficiently than small strains which have characteristically low caloric intakes. From the observed relationships, Morris (1968) developed a formula that predicts the expected daily caloric intake for any given level of dietary energy, given a knowledge of the caloric intake of the strain when fed some standard diet:

$$Y = Y_{2,700} + (0.0005465)Y_{2,700} - 0.1466)(X - 2,700), \qquad (5)$$

where *Y* is predicted energy (kcal/bird/day), $Y_{2,700}$ is characteristic energy intake when the diet contains 2,700 kcal of ME/kg, and *X* is actual dietary energy (kcal/kg).

Leeson et al. (1973) observed that the equation of Byerly (1941) predicts a feed intake about 15 percent higher than that observed for many commercial hybrid laying flocks. They reported a modified partition equation describing feed intake. Balnave et al. (1978) reported equations for minimum AME intakes for laying hens based on an assumed efficiency of 75 percent for the use of ME in egg formation. They reported the following equations for use in estimating daily ME requirements. For egg-producing strains:

$$\mathrm{ME}_{\mathrm{min}} = 388W^{0.75}e^{0.027(22 - T)} + 8.67E. \qquad (6)$$

For meat-producing strains:

$$\mathrm{ME}_{\mathrm{min}} = 450W^{0.75}e^{0.027(22 - T)} + 8.67E \qquad (7)$$

where $\mathrm{ME}_{\mathrm{min}}$ is the minimum ME requirement (k J/day), *W* is body weight (kg), *E* is egg product (g/day), and *T* is environmental temperature (°C). These formulas do not include any requirement for body weight gain. Pullets entering production or on the verge of entering the peak laying period will require an additional allowance for weight gain, however. Balnave and associates (1978) suggest that an allowance for gain may be calculated by assuming an ME requirement of 8 kJ/g of body weight gain.

The National Research Council (NRC; 1981) examined the results of several published studies and derived an equation to estimate the AME intake of laying hens:

$$\mathrm{ME} = 130W^{0.75} \pm (1.015)(\Delta^t) + 5.50\,\Delta W + 2.07\mathrm{EE}, \qquad (8)$$

where *W* is body weight (kg); ^{t} is the difference between 25°C and the ambient temperature, W is growth rate or rate of loss (g/day), EE is egg product (g/day). The equation has since been modified (NRC, 1984) to read:

$$\mathrm{ME} = W^{0.75}(173 - 1.95T) + 5.5\Delta W + 2.07\mathrm{EE}, \qquad (9)$$

where *T* is ambient temperature (°C).

ESTIMATING FEED INTAKE OF BROILERS

Nutrition studies designed to directly examine daily feed or dry matter intake of broilers have been very limited in number. Since broilers are generally fed ad libitum the primary objectives in research have been to examine the response to different diets at some fixed point associated with final market weights, rather than to characterize feed intake. However, there have been some excellent reviews that have examined the literature and made some estimates of the effect of dietary energy level on rate of food intake.

Fisher and Wilson (1974) reviewed more than 160 published research reports on the influence of ME content of the diet on body weight gain and feed consumption. From these data they derived response relationships that allow an estimate of consumption from the dietary energy content, assuming that other nutrients are not limiting. Waldroup et al. (1976) developed equations to predict changes in feed consumption associated with changes in dietary nutrient density level.

In these and other, similar papers, the effect of energy on food consumption has been examined in an indirect manner. With the growing interest in modeling of poultry growth and performance as a means of predicting nutrient requirements, emphasis has been directed toward estimating the energy required to support a given rate of gain established by the genetic potential of the bird. These estimates have generally been divided into three major areas: (1) energy needed for maintenance of body weight; (2) energy needed per gram of tissue synthesized; and (3) modifications due to environmental temperature.

Hurwitz et al. (1978) calculated the maintenance energy of the male broiler-type chick to be 1.91 cal/$g^{0.66}$, with an energy requirement for growth of 2.05 cal/g of gain. Robbins and Ballew (1984) found the maintenance needs of the broiler chick from 8 to 22 days posthatching to be 153 kcal of ME/$kg^{0.75}$ and 190 kcal of ME/$kg^{0.75}$ from 28 to 42 days posthatching. Using these data, the daily energy needs of a growing broiler chick maintained in a thermoneutral environment can be estimated. From this estimate, a daily dry matter intake can be calculated based upon knowledge of the ME and dry matter content of the diet. Hurwitz et al. (1980) have confirmed the results of their estimates in feeding trials.

CALCULATIONS OF DRY MATTER INTAKE

Using equations 1, 2, 8, and 9 given above and typical production standards, estimates of daily dry matter consumption have been made for laying hens (Table 4-1) and broilers (Table 4-2). These are based on the use of a diet containing 2,890 kcal of ME/kg for laying hens and a diet containing 3,200 kcal of ME/kg for broilers, each with a 12 percent moisture content. These values are typical of the majority of feeds used for broilers and laying hens in the United States and other major poultry-producing countries.

TABLE 4-1 Estimated Dry Matter Intake of Laying Hens at Different Stages of Egg Production

Age (weeks)	Egg Production (%)	Egg Weight (g)	BW (g)	Daily Gain (g, approx.)	Dry Matter Intake (g/day) at 25°C Estimated by the Following Equations:[a]			
					1	2	8	9
20	5.0	47.7	1,317	7	60.2	56.0	59.7	61.9
24	62.0	50.7	1,513	6	82.2	78.2	81.5	83.9
28	91.0	55.0	1,653	6	98.0	94.1	96.7	99.3
32	89.0	57.6	1,737	3	93.2	89.4	94.6	97.2
36	87.0	59.3	1,821	2	92.6	88.8	95.1	97.9
40	85.0	60.4	1,877	0	88.5	84.9	93.0	95.8

[a] Based on the following equations for estimating food or energy intake, using a diet with 2.89 ME kcal/g and 12 percent moisture: Equation 1, $F = (0.534 - 0.004T)W^{0.653} + 2.76\ W + 0.80EM$ (Byerly et al., 1980); Equation 2, $F = (0.259 - 0.00259T)W^{0.75} + 2.76\ W + 0.80EM$ (Byerly et al., 1980); Equation 8, $ME = 130\ W^{075} \pm (1.015)(\ _t) + 5.50\ W + 2.07EM$ (NCR, 1981); Equation 9, $ME = W^{0.75}(173 - 1.95T) + 5.5\ W + 2.07EM$ (NRC, 1984), where F is feed/hen/day (in g); T is the ambient temperature (in °C); T = difference between 25°C and ambient temperature; W is liveweight (in g); W is daily change in liveweight (in g); and EM is egg mass/hen/day (in g).

TABLE 4-2 Estimated Dry Matter Intake of Broilers at Different Ages

Age (days)	BW (g)	Daily Gain (g, approx)	Estimated Energy Needs[a] (ME kcal/day)			Daily Consumption of Air-Dry Feed (3.2 ME kcal/g)	Daily Dry Matter Intake (g) (12% Moisture)
			Maintenance	Gain	Total		
7	130	27	47.4	55.3	102.7	32.2	28.3
14	320	34	85.9	69.7	155.6	48.6	42.8
21	560	43	124.4	88.1	212.5	66.4	58.4
28	860	56	165.1	114.8	279.9	87.5	77.0
35	1,250	63	211.3	129.2	340.5	106.4	93.6
42	1,690	59	257.8	120.9	378.7	118.4	104.2
49	2,100	60	297.6	123.0	420.6	131.4	115.6

[a] Based on the following equation of Hurwitz et al. (1978): ME (kcal/day) = 1.91 BW 0.66 + 2.05 W, where BW is body weight (in g) and W is daily gain (in g).

SUMMARY

It is apparent that poultry researchers have not been as concerned about dry matter intake as those working with other animal species. With the growing interest in modeling as a means of estimating nutrient requirements, additional data will undoubtedly be developed with regard to ME needs. Since it is likely that poultry will continue to be fed diets based largely on low-moisture ingredients, accurate estimates of dry matter intakes for these animals will be obtained primarily through knowledge of energy consumption.

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5

Dairy Cattle

INTRODUCTION

Variability in feed intake among dairy cattle introduces an assortment of complex biological problems. Many of these have not been effectively delineated for dairy cattle; nevertheless, insights and measurements made in the past two decades have resulted in several functional predictive equations, with specificity for the physiological function mimicked through models (Mer-tens and Ely, 1979).

In the presence of enough feed, energy for lactating effects the largest change in feed intake above that for maintenance (Bull et al., 1976; Murdock and Hodgson, 1979; Baile and Della-Fera, 1981; Moe, 1981). Other changes arise from weight gain or loss, gestation, activity, and climate (Moe, 1981). Feed intake can be predicted as a function of these independent variables within a lactation period if the energetic efficiency is known and the period of time under consideration is longer than 30 days so that short-term rhythmic changes in intake are averaged (Conrad, 1966; Bines, 1976; Bull et al., 1976; Moe, 1981). However, knowledge of the bounds of the homeorhetic status of cattle and physical constraints on feed intake are significant requirements for developing a prediction equation of feed intake (Conrad et al., 1964; Campling, 1970; Baile and Della-Fera, 1981).

Cows receiving diets with sufficient protein eat 2 to 3.8 times the maintenance requirement for minimal activity (confinement housing) (Ekern, 1972; Tyrrell and Moe, 1975). If the proportion of grain fed is large, dry matter consumption may exceed 4 times maintenance partly because of increased milk production and partly because of the suppression in digestibility (Moe et al., 1965). The suppression in digestibility occurs mostly in the rumen (Tyrrell and Moe, 1975) and may be corrected in part by providing additional crude protein in the diet either as protein (Tyrrell and Moe, 1980) or urea (Huber, 1975; Poos et al., 1979). The reduction in digestibility is about 4 percent per multiple of maintenance increase in intake (National Research Council [NRC], 1978).

LACTATION RESPONSE

Feed intake response of cows to increased milk production in early lactation is slow but normally reaches a maximum between 10 and 14 weeks postpartum as less body stores of fat (Ronning and Laben, 1966; Flatt et al., 1969) and amino acids in muscle (Trigg et al., 1981) are secreted in milk. The rise in feed intake during early lactation may be enhanced additionally by providing a high level of protein (Egan and Moir, 1965; Conrad et al., 1977; Roffler and Thacker, 1983).

The feed intake curves of cows eating mixed rations averaged biweekly for the lactation period are readily fitted to quadratic equations for generalization (Stone et al., 1960; Odwongo and Conrad, 1983); however, the results with individual cows produced spurious deviations from the quadratic curves, presumably representing animal-diet interactions in the feed or environmental constraints on the cows. The change in feed intake for the time course of a lactation period is shown for 14 Holstein cows producing 8,100 kg of milk in 305 days (Figure 5-1). The equation for those data was:

$$I = 11.21 + 0.11d - 0.0003d^2, \qquad (1)$$

where I is kilograms of dry matter per day, and d is days after calving.

The "rules of the thumb" commonly used to estimate feed intake of mature cattle are as follows: (1) nonlactating cattle gaining about 800 g daily eat dry matter equivalent to 2 percent of their body weight, and (2) lactating cows eat dry matter equivalent to 3.2 percent of their body weight. The difference in the caloric density of the food accounts for part of the narrow difference between the two. Monteiro (1972) developed a dynamic model for appetite control during lactation. He used a closed-loop scheme, thereby eliminating consideration of physical limits on feed intake. He reasoned that these limits were of relatively short duration and cows would adjust quickly to a new physiological state in which metabolic controls determined the limits of feed intake. The model is dependent on the input of three independent variables, maintenance requirement, milk production, and gain, but does not account for differences in chemical energy and physical structure of feeds. It is characterized by delay functions for feed intake while cows are transferring body stores of fat and muscle to milk. The equation was:

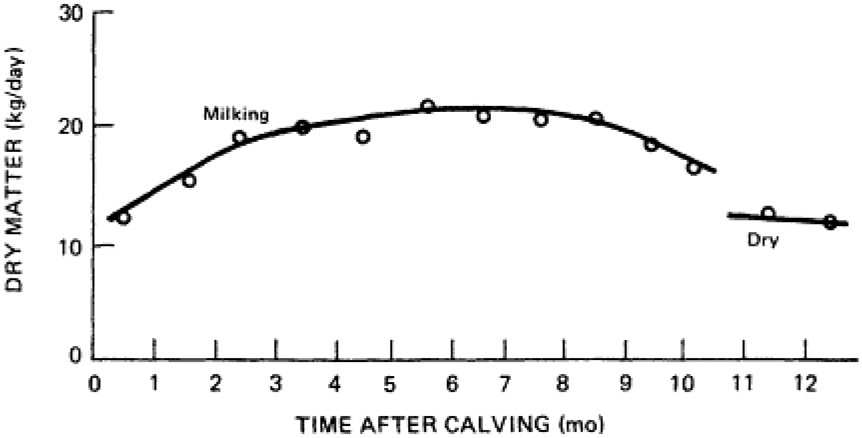

Figure 5-1
Feed intake of Holstein cows during and after lactation.

$$F_t = \beta W_t + \alpha M_t + \gamma \sum_{i=1}^{t} (B_{t-i+1} - B_{t-i})(1-\omega^i) - \rho \sum_{i=1}^{t} (M_{t-i+1} - M_{t-i})\theta^i, \qquad (2)$$

where W_t and its coefficients are weight-based maintenance functions; M_t is milk at any time *t;*   is the weight change;   is the conversion factor of weight into milk;   is the delay factor for gain;   is the delay parameter for milk; and   is the coefficient for evaluating the food deficit not attributable to weight change.

Monteiro (1972) noted that the delay parameters were relatively constant and could be set at 0.65 and 0.80, respectively, for milk and gain. In this computation the delayed lactation represents the amount of milk the cow would produce if there was an instantaneous linear relationship between milk and feed intake. The difference between observed and delayed lactation curves measures successively the deficit or excess in feed intake over milk production and/or gain in weight. Appropriate constants have not been developed for breeds and diets used in the United States.

Although it is difficult to predict feed intake measured as dry matter or digestible energy, the approaches to this problem are worthy of comparison before a method of computing estimates is selected.

LIMITING FORAGE INTAKE

The voluntary intake of different foods and the amount of digesta in the reticulorumen are interdependent (Campling, 1970). When sheep were offered several roughages such as hay and dried grass, there was evidence that they ate to a constant fill (Blaxter et al., 1961). The importance of plant cell wall as the primary restrictive determinant of intake has been demonstrated by Mertens (1973). Presently, the concentration of neutral detergent fiber (NDF) for optimum milk fat production is under investigation in several laboratories.

It is generally assumed that intake and digestibility of forages are directly related, as in equations 5, 6, and 7 cited below. While they are somewhat interrelated, intake and digestibility of forages are separate measures of quality. Intake is dependent upon the structural volume measured by the cell wall content, while digestibility is dependent on the chemical content and its availability (VanSoest, 1982). This is particularly noted if one compares the differences in intake of grasses and legumes. To date no one has devised a successful mathematical model for evaluating on a chemical basis the differences in intake among all forage species, except by using a standard animal for comparing fill. Nevertheless, the mathematical model is an important consideration. Using alfalfa, timothy hay, and orchard grass, Conrad et al. (1964) found that the variance attributable to forage differences might be as high as 43 percent of the total dry matter intake.

A major constraint to feed intake in ruminant foods is the indigestible dry matter (Crampton, 1957; Conrad, 1966; Baumgardt, 1970; Campling, 1970; Mertens, 1985). The relationship between available nutrients and voluntary food intake in ruminants is biphasic (Forbes, 1977). There is a positive correlation between the content of available energy and the amount of food eaten with poor- and medium-quality roughages and a negative correlation with high-quality roughages and cereal-based diets (Conrad et al., 1964; Baumgardt, 1970; Bull et al., 1976). When physical limitations of gut capacity set an upper limit for food intake, predictability is complicated by individual differences in the amount of abdominal space and competition for space by increasing abdominal fat and fetal growth (Campling, 1970; Baile and Forbes, 1974). Conrad et al. (1964) found that all variables associated with the rate of passage of fecal dry matter accounted for 42 percent of the variation in feed intake.

Forbes (1977) developed a computer analog model for predicting variations in feed intake of lactating and/or pregnant cows using metabolic, physical, and endocrine factors. A more sophisticated dynamic model is under development by Mertens and Ely (1979). Neither of these dynamic models has advanced to a state of art for general usage.

Hibbs and Conrad (1975) developed equations to estimate dry matter intake, maximum feed intake, and minimum allowable digestibility. They have been modified here to include newer terms for energy requirements for lactation maintenance and activity and weight gain (Moe, 1981). The requirements for net energy are:

$$NE = 0.080W^{0.75} + 0.74M + 5.1\Delta W \text{ for cows gaining weight} \qquad (3)$$

or

$$NE = 0.080W^{0.75} + 0.74M - 4.9\Delta W \text{ for cows losing weight,} \qquad (3a)$$

where NE is net energy lactation in Mcal, W is body weight in kg, M is 4 percent fat-corrected milk in kg, and W is weight change in kg/day.

NE may be converted to metabolizable energy (ME) by dividing NE by 0.60, which is the proportion of ME converted to milk. ME can be converted to digestible energy (DE) by dividing ME by 0.83, which accounts for losses as methane and in urine from DE. DE can be determined from NE by multiplying by 2.0 (1/0.60 × 1/0.83).

$$DMI_e = 2\,(0.08W^{0.75} + 0.74M + 5.1\Delta W)/4.4, \qquad (4)$$

where DMI_e is dry matter intake needed for energy utilization. When physical factors limit feed intake, then the amount consumed is (Conrad, 1966):

$$DMI_f = \frac{5.4W}{500(1 - dE)}, \qquad (5)$$

TABLE 5-1 Comparison of Intake Predictions (percent of BW/day) for a Cow Weighing 600 kg with Zero BW Changes

4% Fat-Corrected Milk (kg)	Equation Reference No.[a]					
	1	2	3	4	5	6
10	2.2	2.53	2.12	—	2.50	2.42
15	2.4	2.69	2.42	2.25	2.82	2.77
20	2.7	2.87	2.72	2.55	3.09	3.03
25	3.0	3.03	3.02	2.84	3.32	3.22
30	3.2	3.20	3.32	3.13	3.50	3.46
35	3.4	3.37	3.56	3.43	3.64	3.57
40	3.6	3.53	—	3.72	3.74	3.74
45	3.8	3.70	—	3.94	3.79	3.89

[a] Equation reference numbers are as follows:
1. National Research Council (1978).
2. Agricultural Research Council (1976).
3. Theoretical equation predictions for average grass (65% NDF); Mertens (1985).
4. Theoretical equation predictions for average legume (50% NDF); Mertens (1985).
5. McCullough (1981).
6. Odwongo and Conrad (1983).

where DMI_f is dry matter intake in kg/day, W is body weight in kg/day, and dE is the proportion of digestible energy in the dry matter. Maximum feed intake (DMI_{max}) is:

$$DMI_{max} = \frac{5.4W}{500} + \frac{2(0.08W^{0.75} + 0.74M + 5.1\Delta W)}{4.4\ \text{Mcal/kg}}. \qquad (6)$$

Minimum allowable digestibility (DMD_{min}) is:

$$DMD_{min} = \frac{2}{F_{max}I}\,\frac{(0.08W^{0.75} + 0.74M + 5.1\Delta W)}{4.4\ \text{Mcal/kg}}. \qquad (7)$$

Bull et al. (1976) concluded that most cattle eat amounts approximating the maximum feed intake set by ballast constraints. Mertens (1985) has devised a method of predicting feed intake using the amount of NDF. This method appears promising but underestimates the feed intake of cows eating legumes at production levels below 30 kg. A table of comparison abstracted from Mertens' (1985) compilation is presented in Table 5-1.

COMPUTING ESTIMATES OF DRY MATTER INTAKE

Recently Odwongo and Conrad (1983) introduced a prediction equation which provides for changing relationships among amount of milk produced, weight gain or loss, amount of feed needed for maintenance, and intake. Thus,

$$DE = 0.453\,W^{0.593}\,M^{0.33}\,e^{0.16\Delta W}, \qquad (8)$$

For nonlactating pregnant cows the equation is:

$$\mathrm{DE} = 0.453\,W^{0.593}\,e^{0.19\,\Delta W}. \qquad (9)$$

where e is the base of the natural logarithm for Win kg/ day. $\mathrm{DMI_f}$ divided by the concentration of DE (Mcal/ kg) in DM provides feed intake. Validation and efficacy of predicting dry matter intake using Equation 8 is shown in Table 5-2.

Weights of cows were taken monthly; thus, predictions are extremely useful in the long term, but predictions in the short term (per week or per day) may have more error and may not coincide.

None of these equations provides for evaluation of olfactory factors, climate, or changing hormonal effects. Because of the complexity of the control of feed intake and its interrelationship with energy balance, prediction equations of feed intake are limited guides when applied to specific situations. The specific limits arise from environmental, managerial, and social factors; previous feeding history; physiological condition and hormonal status; the physical and nutritional qualities of feed; and several sensory inputs, all of which can have marked effects on feed intake (Baile and Della-Fera, 1981).

Environmental Temperature

Feed intake declines in cattle of European origin, *Bos taurus*, above environmental temperatures of 20 to 25°C (Kleiber, 1975). The decline approximates 3.3 percent/°C. Continuous heat stress may reduce feed intake until cattle reach negative energy balance, and they may cease eating when climatic temperatures above 40°C are maintained. Thermal stress is more severe in early lactation among cows producing large amounts of milk (McDowell, 1972). These effects are enhanced directly by relative humidity. Cold temperatures result in increased feed intake in direct proportion to energy balance, which is affected by tissue insulation, including fatness and pelage (NRC, 1981). Thyroid function and maintenance requirements usually increase from normal at 10°C to 1.5 times maintenance at -20° C (NRC, 1981). Thus the dry matter intake of a cow in weight equilibrium requires 3 additional kg of dry matter at -20° C.

In addition to dietary dilution with indigestible material and hot climate there are numerous other constraints on feed intake. Ruminants have, in comparison to carnivores, dietary regimens that induce large thermogenic effects (Baile and Della-Fera, 1981). Most of this arises from ruminal fermentation as the heat of fermentation. Hypothalamic temperature increases with feeding activity whether or not energy is consumed. It is not likely, then, that hypothalamic temperature plays a role in controlling feed intake. Other factors in the rumen and reticulum influencing feeding behavior are tension receptors (Campling, 1970; Grovum, 1979), osmolarity, pH, and volatile fatty acids (Baile and Forbes, 1974).

Metabolites

Large amounts of volatile fatty acids are produced in the rumen (Baile and Forbes, 1974). Intraruminal injections of acetate or propionate solutions of increasing incremental concentrations before and during a scheduled meal depressed feed intake in cattle, sheep, and goats. The surface of the dorsal area appears to be sensitive to acetate. With as little as 5 percent of the surface exposed to a 1-M solution of acetate, individual meal quantity and length were depressed. Despite the similarity of effect with exposure to acetate and propionate, the receptor sites must be different. Apparently, the receptors for propionate are in the walls of the rumen vein (Baile and Forbes, 1974). While glucose has long been considered a controlling system for feeding in monogastric animals, it is doubtful whether it has a role in cattle. It is interesting, however, that Stone (1975) was able to completely satiate the need of sheep for hay by driving the plasma glucose level to about 130 mg/dl. Likewise there is no specific evidence to date that free fatty acids or amino acids provide satiety signals to cattle consuming balanced diets. It is quite clear, however, that feeding of higher levels of protein at peak lactation stimulates feed intake (Roffler and Thacker, 1983). Feed intake may be summarily reduced during metabolic diseases such as milk fever, ketosis, D-lactic acidosis, or bloat (Baile and Della-Fera, 1981). Infectious mastitis, metritis, and diarrhea either abruptly or chronically reduce feed intake and cause major losses in milk production (Natzke, 1981).

In cattle estrogen (17- -estradiol) administered at peripartурient levels depresses feed intake; this is counteracted by progesterone (Muir et al., 1972). Insulin levels change during feeding (Chase et al., 1977), but its importance or functional response remains undetermined. However, most hormones affect feed intake when given in large amounts, such as the increases in feed intake when surfeit amounts of growth hormone are given (Baile and Della-Fera, 1981).

Meals and Meal Patterns

The microstructure of eating behavior in cattle as measured by periodicity, amount, and rate is an impor

TABLE 5-2 Validation of Various Equations for Predicting Dry Matter (DMI) and Digestible Energy (DEI) Intake of Lactating Cows Using Independent Data

						Concentration of DE						
Diet	Mean Day of Lactation	No.	DMI (kg/ day)	Grain Concentrate (%)	DE: DM Ratio	Maintenance (kcal/g)[a]	Ad libitum (kcal/g)[b]	Predicted DM (kg/day)	Residual DM (kg/day		(%)	r^2
Corn silage and grain concentrates[c]												
Group #1	16	15	22.86	67	3.77	3.29	3.01	21.01	1.85	8.07	13.07	0.139
Group #2	16	15	21.32	67	3.55	3.33	3.06	19.39	1.93	9.05	10.70	0.131
Group #3	16	15	18.49	67	3.28	3.33	3.14	18.43	0.06	0.32	10.52	0.435
Group #4	16	15	22.74	67	3.68	3.33	3.07	22.95	-0.21	0.92	13.95	0.478
Group #5	38	15	24.14	67	4.14	3.29	2.99	24.72	-0.58	2.40	11.33	0.173
Group #6	38	15	22.48	67	3.74	3.33	3.06	22.26	0.22	0.98	13.36	0.455
Group #7	38	15	19.36	67	3.50	3.33	3.10	18.85	0.51	2.63	7.59	0.196
Group #8	38	15	22.70	67	3.70	3.33	3.07	22.94	-0.24	1.06	12.14	0.418
Alfalfa silage and grain concentrates[d]	140	34	22.91	45	3.83	2.92	2.81	22.73	0.18	0.78	8.40	0.607
Alfalfa silage and grain concentrates[e]	103	27	20.31	33	3.62	2.95	2.85	20.84	-0.53	2.60	8.30	0.366
All cows, mean			21.73	61.40	3.69	3.24	3.02	21.41	0.32	2.88	10.94	0.34

NOTE: Based on the following equation of Odwango and Conrad (1983): $DE = 0.453\ W^{0.593} M^{0.33} e^{0.16\ \ W}$, weights in kg and energy in Mcal.

[a] National Research Council (1982).

[b] Reduction from adjustment for feed intake above maintenance as -4% per multiple above maintenance and 0.25% reduction in digestibility for each percent point of grain concentrate above 33% (Moe, 1981; Tyrrell and Moe, 1975).

[c] This study was conducted for an 11-day period.

[d] This study was conducted for a 70-day period.

[e] This study was conducted for a 70-day period.

SOURCE: L. D. Satter, University of Wisconsin, Madison, personal communication, 1983.

tant feature of eating behavior in cattle. These measures are essential to understanding the interaction of a specific feed with an experimental animal.

The time required for satiation is highly variable and dependent on the diet. After a hiatus in eating, cows may eat a meal of palatable concentrate within 15 min, whereas to eat a total mixed ration with silage containing fermentation products, 150 min may be required before the animal ceases with nibbling bouts (Conrad et al., 1977; Heinrichs, 1982). In general, the rate of eating during the first bout of newly administered feeds resulted in successively increasing meal times for wetted concentrate, silage, and hay (Conrad, 1966). In cattle, as in other species, there is a post-prandial correlation, that is, a significant correlation between the size of a meal and the interval that follows it. Typically, in cattle fed once or twice daily there are two large meals that may occur as a normal meal—when fresh food is given and immediately after milking. The average time for spontaneous meals is about 5 min, during which cows eat about 600 g. Normally, cows consume 10 to 20 spontaneous meals during 24 h. The initial meals are closely related to the physical form of the diet due to differences in degree of mastication and deglutition that are required (Kertz et al., 1981). This may also be important in spontaneous meals. Gustatory, olfactory, or tactile stimuli can also influence the amount of total feed intake and feeding patterns in cattle.

Three classes of compounds have been found to shorten meal length and meal weight. They are organic acids, amines, and ammoniacal nitrogen or its precursors (Clancy et al., 1977). Because of widespread use of silage which contains all of these compounds, knowledge of their quantitative effects has become of interest. The reduction in meal length which coincided with ammonium load in the rumen as a result of injection of ammonium salts or precursors of ammonia showed that ruminants were perturbed quickly, possibly from intracellular acidification and intoxication by the increasing ammonia concentration in the rumen (Conrad et al., 1977). When this was done with urea, the resultant effect was malaise and learned avoidance (Chalupa et al., 1979; Kertz et al., 1982). Carotid blood ammonia concentration increased so rapidly after dosing with urea that it was apparent that the ammonia absorbed from the rumen leaked past the liver (Bartley et al., 1981). Thus an alternative site for the action and source of malaise may be from a direct effect of ammonia on the central nervous system.

Amine nitrogen depresses meal length in a similar manner; however, the site of the effect is not known (Clancy et al., 1977; Phillip and Buchanan-Smith, 1982).

Grinding and Pelleting

In mature cows principally offered roughage diets containing adequate protein, control of feed intake by physical factors in the rumen usually ceases between 60 and 70 percent digestibility (Conrad et al., 1964; Montgomery and Baumgardt, 1965). Grinding the diets alters the threshold of digestibility downward to a point at which physical limitations may cease to exist (Campling, 1970). However, there does appear to be a total gut limit in lactating cows and dairy heifers which is 22 percent higher when ground diets are fed (Montgomery and Baumgardt, 1965; Bull et al., 1976). This approximates what would be expected if the space in the cecum and large bowel was added to the ruminal space for the pool of indigestible material. Thus, the daily turnover rate of fecal dry matter rises from 1.08 percent body weight (Conrad et al., 1964) to 1.32 percent (Bull et al., 1976). In rats, it is 1.4 percent body weight (Adolph, 1947). This is commensurate also with the observation that grinding and pelleting of the diet result in an increased fecal mean particle size from 0.30 to 0.36 mm and more rapid evacuation from the gut. Thus, in general, dairy cattle consume 20 percent more dry matter of ground and pelleted diets if they do not contain chemical inhibitors such as urea, fatty acids in fat, and alkaloids or if the resultant pellet is injurious to the mouth (Montgomery and Baumgardt, 1965; Hibbs and Conrad, 1975).

SUMMARY

In the metabolic partitioning of feed, cows expend a sizable portion of energy for maintenance of temperature regulation. Periodically, excess heat may accrue from the high calorigenic effect of fibrous feeds, causing reduced feed intake. Lactation, growth, and fattening are all stimuli for increased feed intake. Under conditions of normal temperature and humidity, these are quantitative effects that can be related functionally to body size. There is a consensus that at low digestibilities, the level of milk production is determined by the cow's capacity for feed, particularly undigested residues, and the rate at which undigested feed can be moved through the alimentary canal. At high levels of digestibility, the physiological state of the cow is the primary determinant of feed intake. The point among a series of increasing digestion coefficients at which physical limitations on eating capacity vanish and the influence of productive energy demands become dominant varies with body size, production, and amount of fecal dry matter excreted daily. Equations 4 through 7 can be used to approximate this point.

TABLE 5-3 Predicted Dry Matter Intake (DMI) in Dairy Cows

Milk, 4% FCM (kg/d)	Change in weight (kg/d)	DE in Diet (Mcal/ kg)	Body Weight (kg)									
			350	400	450	500	550	600	650	700	750	800
15	1.0	2.85	*	*	*	18.2	19.3	20.3	21.3	22.2	23.2	24.1
	1.0	3.10	13.4	14.7	15.7	16.8	17.7	18.7	19.6	20.5	21.3	22.1
	0.5	2.85	*	*	15.9	16.9	17.9	18.8	19.7	20.6	21.5	22.3
	0.5	3.10	12.5	13.6	14.6	15.5	16.4	17.3	18.1	18.9	19.7	20.5
20	1.0	2.85	*	*	*	*	*	22.3	23.4	24.5	25.5	26.5
	1.0	3.10	*	*	*	18.5	19.5	20.6	21.6	22.5	23.5	24.4
	0.5	2.85	*	*	*	18.6	19.7	20.7	21.7	22.7	23.7	24.7
	0.5	3.10	13.8	14.9	16.0	17.1	18.0	19.0	20.0	20.9	21.8	22.7
25	0.5	2.85	*	*	*	*	*	22.0	23.1	24.2	25.2	26.2
	0.5	3.10	*	*	*	18.2	19.3	20.2	21.3	22.2	23.2	24.1
	0	2.85	*	*	*	*	19.4	20.4	21.4	22.3	23.3	24.2
	0	3.10	13.6	14.7	15.8	16.8	17.8	18.8	19.7	20.5	21.4	22.2
30	0.5	2.85	*	*	*	*	*	*	*	26.0	27.0	28.1
	0.5	3.10	*	*	*	*	20.6	21.8	22.8	23.9	24.9	25.8
	-0.5	2.85	*	*	*	18.0	19.1	20.1	21.1	22.0	23.0	23.9
	-0.5	3.10	13.4	14.5	15.6	16.6	17.6	18.5	19.4	20.3	21.2	22.0
35	0.0	2.85	*	*	*	*	*	*	24.1	25.2	26.3	27.3
	0.0	3.10	*	*	*	*	20.1	21.1	22.2	23.2	24.1	25.1
	-0.5	2.85	*	*	*	*	20.1	21.2	22.2	23.2	24.2	25.1
	-0.5	3.10	*	*	16.4	17.5	18.5	19.5	20.4	21.3	22.2	23.1
40	0.0	2.85	*	*	*	*	*	*	*	*	27.5	28.6
	0.0	3.10	*	*	*	*	*	22.2	23.2	24.3	25.3	26.3
	-0.5	2.85	*	*	*	*	*	22.2	23.3	24.3	25.3	26.3
	-0.5	3.10	*	*	*	18.3	19.4	20.4	21.4	22.4	23.3	24.2
45	0.0	2.85	*	*	*	*	*	*	*	*	*	29.7
	0.0	3.10	*	*	*	*	*	*	24.1	25.2	26.3	27.3
	-0.5	2.85	*	*	*	*	*	*	24.2	25.2	26.3	27.3
	-0.5	3.10	*	*	*	*	20.2	21.2	22.2	23.2	24.2	25.1
55	-0.5	2.85	*	*	*	*	*	*	*	*	*	29.2
	-0.5	3.10	*	*	*	*	*	*	23.8	24.9	25.9	26.9
	-1.0	2.85	*	*	*	*	*	*	23.9	25.0	26.0	27.1
	- 1.0	3.10	*	*	*	*	19.9	21.0	22.0	23.0	23.9	24.9

NOTE: These values are functions of daily milk production (M), change in weight (ΔW), digestible energy (DE) concentration in the diet, and total BW and were computed from the formula DE = $0.453\, W^{0.593} M^{0.33} e^{0.16} \Delta W$ (Odwongo and Conrad, 1983). An asterisk means that the amount of feed computed was in excess of the amount cows would be expected to eat and still maintain a daily turnover of undigestible "gut fill" equal to 1.1% of their BW.

Changes in estimated dry matter intake (DMI) in cows as functions of daily milk production (M), change in weight (ΔW), digestible energy (DE) concentration in the diet, and total body weight were computed from the formula DE = $0.453\, W^{0.593} M^{0.33} e^{0.16\Delta W}$, as indicated in Equation 8. The limits of feed intake were determined with Equation 5. The results are summarized in Table 5-3 for cows of different sizes.

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6

Beef Cattle

INTRODUCTION

The dominant factors that determine dry matter intake of beef cattle are physiological demand due to maintenance needs and potential for production, and limitations in gastrointestinal capacity. Beef cattle are kept in the United States primarily as a means of marketing feed—especially feed with little or no market value. A large proportion of the total intake during the life cycle of beef cattle, therefore, is forage. For the beef cattle herd, voluntary intake must be predicted to determine the proportion of their requirements that can be met from low-quality feeds. Then the absolute amounts of supplemental feeds needed daily can be calculated. During early postweaning growth, calves are typically used to market forages. Although forages fed to calves are of higher quality than those usually fed to the beef herd, most calves fed high-forage diets are not able to consume enough digestible energy to allow physiological demand to control intake because of limits in gastrointestinal capacity. During the finishing period, however, limits in physiological demand for growth can be the dominant factor controlling intake.

The National Research Council (NRC, 1984) emphasizes the expression of nutrient requirements as amounts per head daily. At any particular stage of growth, however, nutrient requirements are related to rate of gain (NRC, 1984), which depends upon intake of the particular diet being fed (Fox and Black, 1984). Therefore, intake must be predicted before the diet can be formulated to meet requirements for growth. With accurate prediction of intake and rate of weight gain, nutrient requirements can be expressed as a percentage of the diet, which may also be more appropriate for describing requirements for rumen fermentation (Fox et al., 1984).

The purpose of this chapter is to identify and discuss the primary factors influencing feed intake of beef cattle and to present equations and adjustment factors that can be used to predict intake under widely varying feeding and environmental conditions. Many producers have predictions for intake from historical information that reflects their ration, management, cattle types typically fed, and environmental conditions. They may wish to only estimate the effect of one variable for which they have no independent data. Therefore, the approach used here will be to present separate equations and adjustment factors for each variable where possible.

PHYSIOLOGICAL FACTORS

Body Size and Production Demands

The relationship of body size to feed intake has been a subject of much debate. Gastrointestinal size is related to the 1.0 power of body weight, while energy intake is related to weight raised to the 0.75 power (VanSoest, 1982). This implies a more rapid turnover of rumen contents at lighter weights. Other studies in which the best fit of intake data with body weight was examined resulted in powers of 0.5 to 0.8 (Colburn and Evans, 1968). Owens and Gill (1982) found intake to be related to the 0.47 power of body weight; Thornton et al. (1985) found that this relationship varied with the time on a high-energy ration. Preston (1972) concluded that intake of beef cattle was 95 g/$W^{0.75}$, with a 95 percent confidence interval of 88 to 102, where W is body weight.

The NRC (1984) developed equations to describe feed intake in beef cattle that reflect intake as a function of the 0.75 power of body weight, as did Plegge et al. (1984) and Fox and Black (1984). Figure 6-1 summarizes the relationship of dry matter intake and dietary energy concentration by comparing systems proposed by the

Agricultural Research Council (ARC, 1980), NRC (1984), Fox and Black (1984), and Plegge et al. (1984). With most diets fed to the breeding herd and during early postweaning growth, cell wall content (neutral detergent fiber) is the dominant characteristic limiting intake. An increase in the dietary concentration of slowly degraded or indigestible material causes a reduction in the rate of passage and physical fill becomes limiting (VanSoest, 1982; Mertens, 1983). As the net energy concentration in the diet is increased, as in finishing diets, at some point metabolic controls become the dominant factors limiting intake (Figure 6-1). The use of dietary energy concentration to describe energy density effects on intake represents the combined effects of rate of passage and metabolic controls on appetite. Procedures for predicting feed energy values from feed analysis have been outlined (Mertens, 1983; NRC, 1984; VanSoest et al., 1984); these procedures can be used to predict dry matter and energy intake.

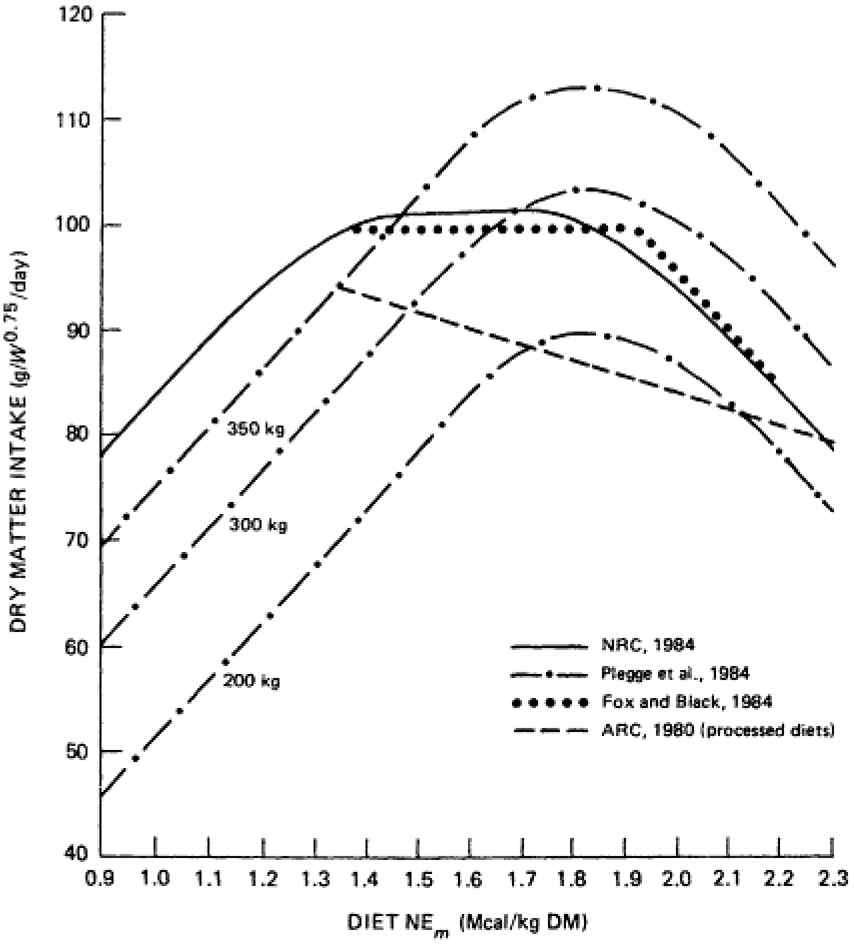

Figure 6-1
Relationship between dietary energy concentration and dry matter intake (DM) in growing cattle. NE_m, net energy for maintenance.

The data of Owens and Gill (1982), Fox and Black (1984), and Plegge et al. (1984) indicate that intake/unit of metabolic weight begins to decline at about 350 kg average-frame-size steer equivalent weight (Figure 6-2). These data indicate that the degree of fatness and/or a reduction in demand for growth influence voluntary intake. Song and Dinkel (1978), using the data of Smith et al. (1976), found a significant decline in intake with degree of maturity. Increased body fat likely reduces appetite as a result of competition for abdominal space (Taylor, 1969) or feedback from adipose tissue (Chapter 1).

It is clear that the effect of body fat on intake must be taken into account. It is especially important when projecting gains at the end of a feeding period to make marketing decisions. The optimum sale weight is projected to be considerably lighter if intake is predicted to decline as body fatness increases. As shown in Figure 6-2, there appears to be additional factors influencing intake at early stages of growth. Fox and Black (1984) found relative intake to be constant until later stages of growth; Owens and Gill (1982) and Plegge et al. (1984) found the weight when growing cattle are started on a high-energy ration to be related to intake patterns over the feedlot finishing period. Further work is needed to describe the basis for this effect.

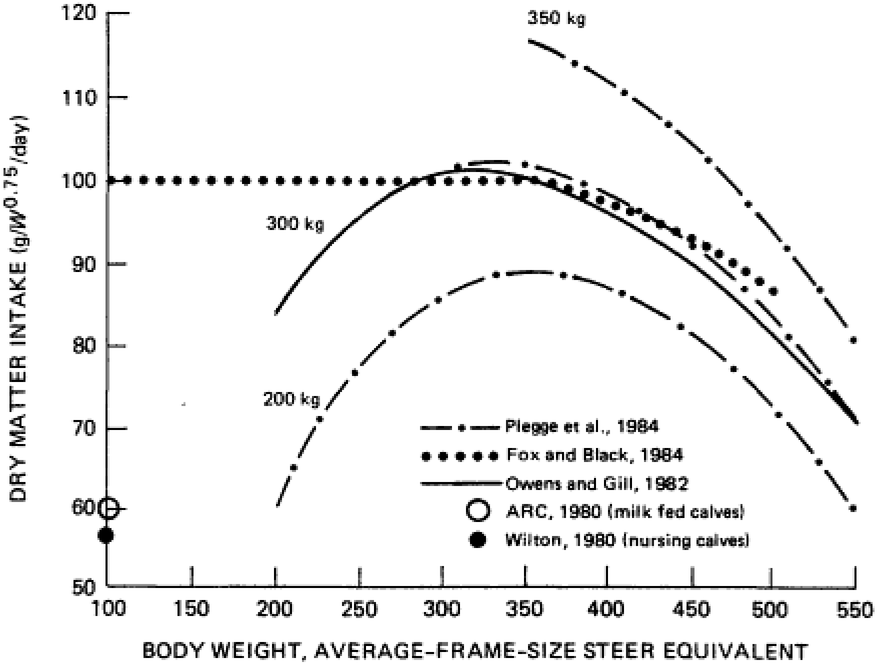

Figure 6-2
Relationship of stage of growth and weight of a steer when placed on a high-energy diet to dry matter intake.

Nursing or milk-fed calves consume less total dry matter than weaned calves. The data of Wilton (1980) and Wyatt et al. (1977) indicate an average total DM intake of 60 g/$W^{0.75}$ for nursing or milk-fed calves consuming 5 to 10 kg of milk/day with access to dry creep feed or calf starter feed. Calves with continuous access to whole milk or milk substitutes at 12 to 15 percent DM consume 70 to 80 g/$W^{0.75}$ but 60 g when fed only twice daily (ARC, 1980). The data of Le Duet al. (1976) indicate a grazed forage DM consumption of 33 g/$W^{0.75}$ at a milk DM consumption of 36 g/$W^{0.75}$, increasing to a forage intake of 101 g/$W^{0.75}$ at a milk DM intake of 6 g/$W^{0.75}$.

The relationships among body size, body composition, and intake discussed previously suggest that mature dry cows may have voluntary intakes similar to those of growing cattle of similar body composition. Beef cows in average flesh condition (condition score 5) contain about 22 percent body fat (George, 1984), suggesting that intake would be expected to be similar to those of calves weighing up to 364 kg. A number of studies (Bines et al., 1969; Taylor, 1969; Lusby et al., 1976; ARC, 1980) indicate that intake of cows is reduced as body fat increases. Lactating cows consume 35-50 percent more than nonlactating cows of the same weight and on the same diet, with an average increase of 0.2 kg of DM/kg of fat-corrected milk (ARC, 1980). Voluntary intake declines by 2 percent per week during the last month prepartum, increases to a peak 4 to 6 months postpartum, and then declines as milk production is reduced (ARC, 1980 and Chapter 5 in this volume). A comparison of the two intake equations of the NRC (1984) with the data from several studies (Streeter et al., 1974; Lusby et al., 1976; Lemenager et al., 1978; Holloway et al., 1979; Horn et al., 1979; ARC, 1980) indicates that voluntary intake of beef cows is similar to that of growing cattle when adjusted for the effect of milk production.

The information presented in this section, considered in light of that presented in Chapter 1, indicates that the primary factors that control intake in beef cattle are those related to direct dietary effects (distension of the rumen wall, rumen pH and acetate concentration, and hepatic uptake of propionate) and metabolic factors mediated by the central nervous system, including size of adipose mass and demand for satisfying maintenance and production functions. Subsequent sections will examine these effects.

Mature Size and Sex

Cattle varying in mature size and sex differ in the weights at which they reach a given degree of fatness (Smith et al., 1976; Byers, 1980; Fortin et al. 1980; Fox and Black, 1984). Thus, they would be expected to dif fer in the weights at which intake/$W^{0.75}$ begins to decline. Harpster (1978) found that heifers corresponding to diverse breed types of steers had 3 percent higher intakes/$W^{0.75}$ when fed to the same stage of growth. Heifers fed to the same finish (percentage of final body fat) as steers consumed 5 percent more in studies by Klosterman and Parker (1976). Growing bulls and heifers had similar intakes/$W^{0.75}$ in the studies of Fox et al. (1984). Ayala (1974) found similar relative intakes among bulls, steers, and heifers. A system for predicting the intakes of cattle varying in frame size and sex has been developed by Fox and Black (1984). Intake for alternative frame sizes is based on that used for an average-frame-size steer of equivalent body composition.

Age

Owens and Gill (1982) found that daily dry matter intake increased 0.20 kg for each 50 kg above 277 kg of initial weight when placed on a high-energy diet, and it decreased by this same amount for initial weights under 277 kg. Similar trends were obtained by Plegge et al. (1984), Ralston et al. (1970), and Thornton et al. (1985).

The NRC (1984) concluded that growing cattle started on feed as yearlings consume an average of 10 percent more than calves with similar weights and frame sizes. Abdalla (1986) found that compensating cattle whose rate of growth had been retarded to about half of that at which maximum daily protein gain could be expected consumed an average of 10 percent more DM/$W^{0.75}$ when placed on a full feed. The yearling effect on intake may be the same as that obtained during compensatory growth, as the cattle's older age for lesser weight indicates a previous period of retarded growth. Abdalla (1986) found that rumen size rapidly increases following retarded growth; the impetus for compensatory growth appeared to be increased demand for nutrients, with an increase in appetite as well as increased efficiency of utilization of nutrients. Field observations indicate that previous diet is a key factor in determining subsequent eating patterns. For example, calves that previously grazed on wheat pasture consume more than calves from drylot feeding backgrounds or drought conditions (D. L. Gill, Oklahoma State University, personal communication, 1985).

Genetic Variance

Reid (1962) suggested that the best opportunity for improving feed efficiency through selection was to select for greater appetite; the likelihood that cattle that could be identified that metabolize consumed nutrients more efficiently was small.

Across four studies (Swiger et al., 1961; Brown and Gifford, 1962; Koch et al., 1963; Brown and Gacula, 1964) heritability estimates reported for feed intake varied from 0.43 to 0.76, with a mean of 0.62. Thus cattle of a given type are likely to vary in their appetite, and intake and gain may be considerably under- or overprojections due to genetic variance. Intake data collected over 9 years from individually fed bull and heifer calves were summarized in which the effects of weight, frame size, sex, and body condition could be separated in a herd of cattle in which selection had been practiced for feed efficiency (D. G. Fox, Cornell University, unpublished data, 1983). Across five frame sizes, intake was 12 to 14 percent greater than predicted by the system of Fox and Black (1984). These data suggest that predicted intake can be increased by 12 to 14 percent for cattle purchased from herds where selection pressure for growth rate independent of frame size or environment is practiced. In these same cattle, feed efficiency independent of intake effects was 18 to 34 percent greater than expected, indicating that progress can be made in intake and use of consumed nutrients by selecting for increased relative growth rate. Increased genetic potential for growth likely stimulates intake as a result of a greater demand for production.

Breed Type

Intake differences among beef cattle breeds and their crosses may largely be accounted for by differences in mature size. Much of the data on this effect were confounded because the cattle were not usually fed to the same degree of fatness and, thus, over the same stage of growth. In the experiments of Smith et al. (1976), crossbreds averaged 2 percent greater intake than straightbreds fed to the same stage of growth. Harpster (1978) and Lomas et al. (1982) did not find any differences in intake/$W^{0.75}$ due to breed types.

Holsteins may be an exception. Examination of a number of studies in which Holsteins were compared with beef breeds (Garrett, 1971; Crickenberger et al., 1978; Thonney et al., 1981) suggest that at the same stage of growth Holsteins consume an average of 8 percent more DM/$W^{0.75}$; similar results were reported by Plegge et al. (1984). However, recent studies (Thonney et al., 1981; Fox and Black, 1984) indicate that this difference disappears at weights beyond 450 kg, and in fact, relative intake of Holstein steers declines at a faster rate with increased fatness than with beef breeds. It can be speculated that the tendency of Holsteins to deposit a higher proportion of their body fat internally may be involved.

It is possible that differences in rearing management between Holsteins and beef breed calves may play a role in the usually higher feed intake of Holsteins during most of the growth period. Beef calves usually nurse cows until at least 7 months of age; Holsteins are weaned by 6 weeks of age, resulting in a higher intake of ruminally fermented feeds at early stages of growth. End products of fermentation stimulate rumen development (VanSoest, 1982). In addition, Holstein steers are likely to be fed a high-forage diet for a relatively long time on dairy farms before being placed on feed in feed-lots. A large part of their higher intake, however, may be due to a high demand for production due to their higher body protein while on feed (Crickenberger et al., 1978) and their higher growth potential (Owens et al., 1985).

ENVIRONMENTAL EFFECTS

Temperature and Weather

The effects of environment on dry matter intake have been summarized (NRC, 1981). The primary environmental effects on voluntary intake of cattle occur at temperatures greater than 25°C and less than 15°C and by exposure to wind, storms, and mud. These effects are summarized in Figure 6-3. Adjustment for these effects is more accurate if the average environmental state for a period of a week or month rather than daily fluctuations is used. Intakes are more variable and difficult to predict under these conditions, especially if the changes are abrupt.

Breed differences in voluntary intake under various environmental conditions have not been clearly identified. However, it appears that intake changes due to environmental conditions vary with changes in the animal's critical temperature (the point at which it must increase or decrease heat production to maintain a normal body temperature). This temperature is a function of age, body mass, hide and external fat thickness, hair coat density and depth, and dietary energy density (NRC, 1981). Thus, shifts of the curve to the right or left in Figure 6-3 for various breed types can be predicted by estimating their deviation from the average critical temperature, which can be calculated as outlined by the NRC (1981).

Photoperiod and Timing of Feeding

Light to dark ratios influence eating patterns (Tucker et al., 1984). Many feedlots illuminate their lots at night,

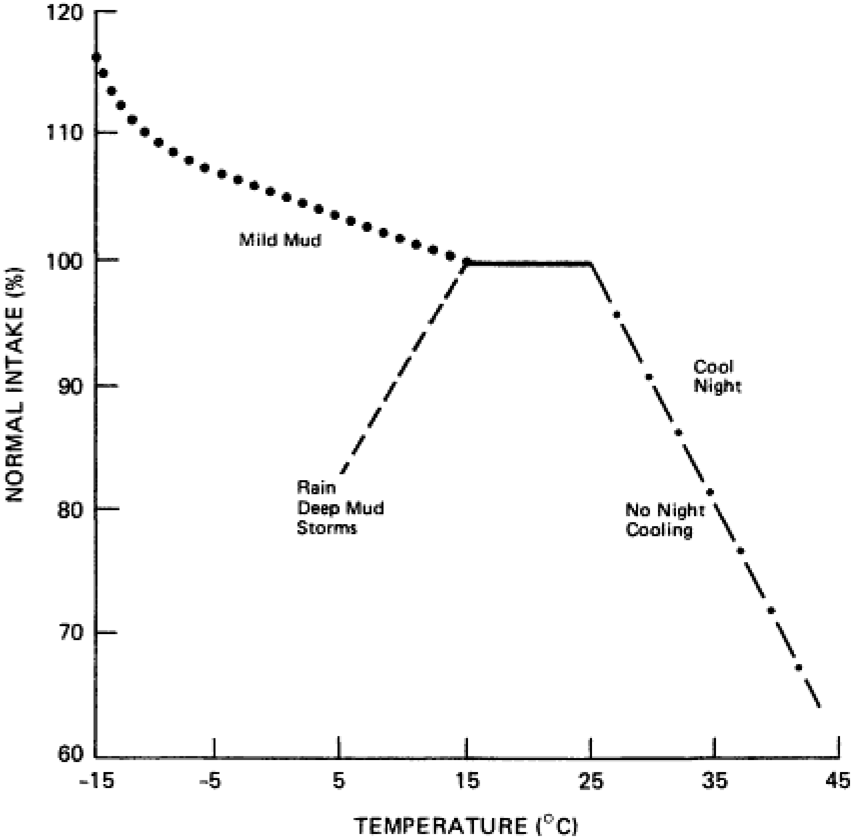

Figure 6-3
Environmental effects on dry matter intake.

with the assumption that it stimulates eating activity. However, there appears to be an optimum ratio of light (L) to dark (D) over a 24-h period. Sheep and heifers have been shown to consume up to 13 percent more feed and grow faster when the ratio is 16L to 8D than when the ratio is 8L to 16D or continuous light (Forbes et al., 1975; Peters et al., 1980; Schanbacher and Crouse, 1980; Petitclerc et al., 1983, Zinn et al., 1983). Heifers and sheep on the 16L to 8D ratio had more total eating events, with more occurring during lighted hours. Heifers on the 8L to 16D ratio increased their eating activity 1 to 2 h before lights came on; those on the 16L to 8D ratio did not reinitiate eating activity until lights were actually on. Eating activity was also stimulated when fresh feed was offered. Eating pattern has been directly related to increased rate of weight gain, however, only when feeding occurs once per day, soon after dawn or in the middle of the day compared to I h before dark (Zinn et al., 1983). Feeding twice daily improved intake 2 percent and daily gain 5 percent across five experiments (Embry and Burkhardt, 1971). Photoperiod appears to have an important effect independent of intake. Short days stimulate fat deposition, while long days stimulate protein accretion in cattle (Tucker et al., 1984).

Forage Availability for Grazing Cattle

The two major factors influencing intake by grazing cattle are quantity and quality of available forage. The quantity of available forage is the first limiting factor. In pastures or ranges with abundant available forage, animals can selectively graze large mouthfuls of the most nutritious plant parts, usually leaves. As the quantity declines, the amount of intake per grazing bite declines. In addition, as the grazing pressure increases and/or the plants mature, the animal is forced to consume plant parts with a slower rate and extent of digestion. A summary of data by Rayburn (1986) indicates that intake of cattle and sheep is maximum at a forage availability of about 2,250 kg/ha, or 40 g of organic matter (OM)/kg of live weight (LW), and then rapidly declines to 60 percent of maximum by 450 kg/ha or 20 g of OM/kg of LW (Figures 6-4 and 6-5).

Pastures containing legumes have usually given higher intakes (Holloway and Butts, 1983; Rayburn, 1986). The rate of digestion for legumes is higher than that for grasses of the same total digestibility (Mertens, 1983; Rayburn, 1986).

The impact of these effects on animal performance and production per hectare on a pasture that begins at ≥2,250 kg of DM/ha is shown in Figure 6-6. Reduction in animal performance is noticeable as 50 percent utilization is reached, but production per hectare is maximized at 80 percent utilization.

DIETARY FACTORS

Diet Water Content

Nonlactating cattle consume an average of 3 parts water to 1 part dry matter up to a 4.4°C environmental

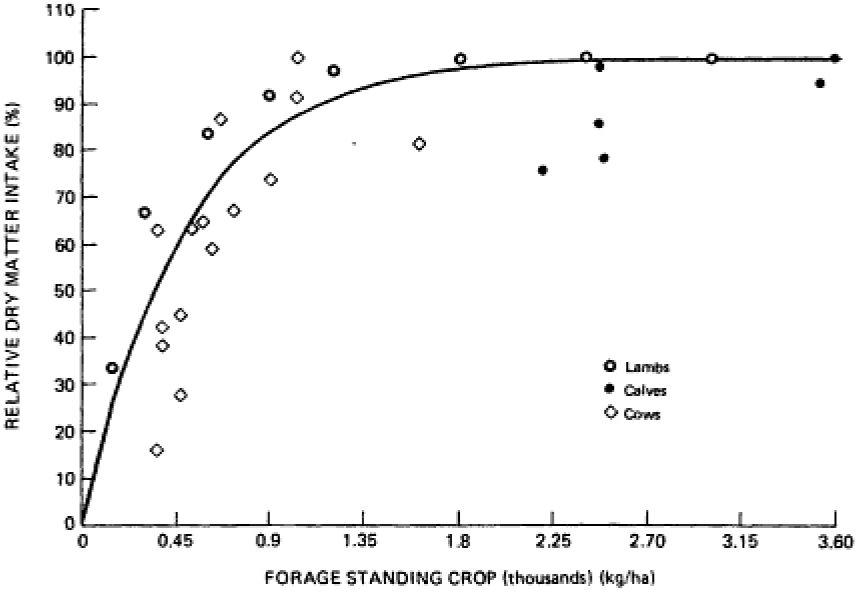

Figure 6-4

Effect of forage standing crop on the relative forage dry matter intake (relative DMI) of lambs, calves, and dairy cows grazing pasture under continuous grazing management (Ray-burn, 1986).

temperature and then an increased amount of water proportional to increases in the ambient temperature (Winchester and Morris, 1956). Thus, restricting water reduces dry matter intake (Utley et al., 1970), and any factor that affects water consumption could reduce intake.

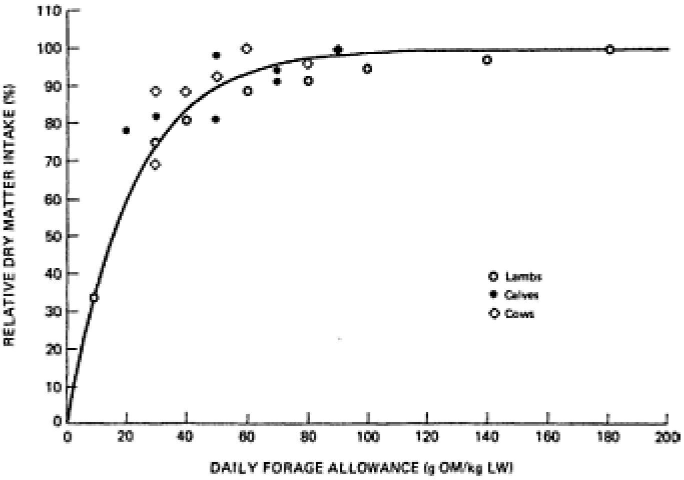

Figure 6-5
Effect of daily forage allowance on the relative forage dry matter intake (relative DMI) of lambs, calves, and dairy cows grazing pasture under rotational grazing management (Rayburn, 1986).

Voluntary free water intake plus water in the feeds consumed is approximately equal to the water requirements of cattle (NRC, 1984). Thus, dietary water concentration per se would not be expected to influence dry matter intake until total expected water intake per unit of dry matter is exceeded.

Rumen contents contain about 85 percent water; water added to the rumen has little effect on dry matter intake since it is rapidly absorbed and excreted (Van-Soest, 1982). The data of Winchester and Morris (1956) can be used to estimate the percentage of water in the total diet intake per day. For lactating cows, 0.87 kg of water must be added to the expected daily intake for each kg of milk produced.

Forced water intake above these levels could reduce intake. In milk-fed calves intake is reduced 32 percent as dry matter content of milk falls from 15 to 5 percent (ARC, 1980).

Degree of Fermentation

When data are corrected for errors in dry matter determination, it has been shown that a desirable fermentation during ensiling does not reduce dry matter intake in cattle (Fox and Fenderson, 1978; ARC, 1980).

However, when silage is unusually wet or dry, unde

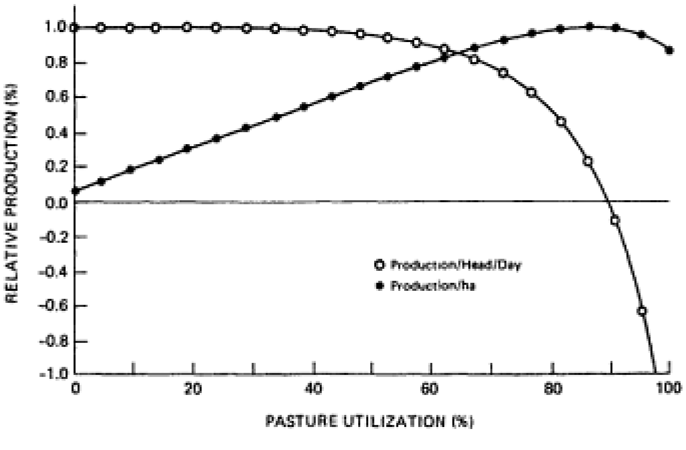

Figure 6-6
Effect of grazing pressure under rotational grazing on relative production (Rayburn, 1986).

sirable fermentation may occur. In silages with greater than 65 percent DM, the potential for molding increases, which could reduce intake (Mertens, 1979). In silages with less than 30 percent DM, a pH of higher than 4.4 may be indicative of proteolytic fermentation and the development of amines and excessive butyric acid, which may reduce intake (VanSoest, 1982).

Dietary Protein

Diet digestibility, and thus rate of passage, is reduced if the nitrogen requirements of rumen bacteria are not met (VanSoest, 1982). Nitrogen requirements for maximum microbial growth are primarily a function of digestible organic matter intake (VanSoest et al., 1982).

Diet protein solubility and degradability influence dietary protein availability to meet microbial nitrogen needs. Thus, the level of nitrogen needed in the rumen to support the maximum rate of passage would be expected to vary with carbohydrate digestibility in the rumen. An evaluation of data from several studies (Figure 6-7) indicated that most diets satisfy this requirement at 6 to 8 percent crude protein, but 9 to 11 percent crude protein may be required for calves, especially when highly digestible forages are the primary diet. Dietary protein can be overprotected to the point where rumen nitrogen requirements are not met (Fox et al., 1984; VanSoest et al., 1984).

Feed Processing

Reducing particle size and collapsing of the cell structure by finely grinding and pelleting fibrous feeds reduces rumination time and increases the rate of passage and thus feed intake (VanSoest, 1982), by up to 50 percent (Greenhaugh and Wainman, 1972). Digestibility can be depressed by up to 3 to 8 percent per increase in multiples of maintenance, but utilization of digestible energy may be improved because the acetate: propionate ratio may be decreased.

The NRC (1984) recently summarized the influence of processing feedstuffs on intake and utilization. They concluded that intake is improved most with processing where roughage is the major constituent, and the impact increases with increasing concentrations of plant cell wall and with alkali, ammoniation, or other treatments that increase the potential for cell wall digestion. Increasing the rate of passage of indigestible material can improve intake of forages high in cell wall content by up to 50 percent. Generally, however, intake is reduced if grains are processed and if digestibility is increased. The ARC (1980) summarized data from six journals to separate out the interaction of diet energy concentration and degree of processing. Based on their summary, the change in intake due to fine processing can be predicted to be 47.2 percent at 0.92 NE_m, 20.8 percent at 1.33 NE_m, 0 at 1.73 NE_m, and -17.2 percent at 2.10 NE_m. These predicted values generally are consistent with the effects suggested by the NRC (1984).

This summary does not attempt to define the optimum degree of processing, as changes in digestibility and the utilization of digestible energy are influenced by processing, and vary with treatment used, age, grain type, and grain variety. The reader is referred to the NRC (1984) for recommendations in this regard.

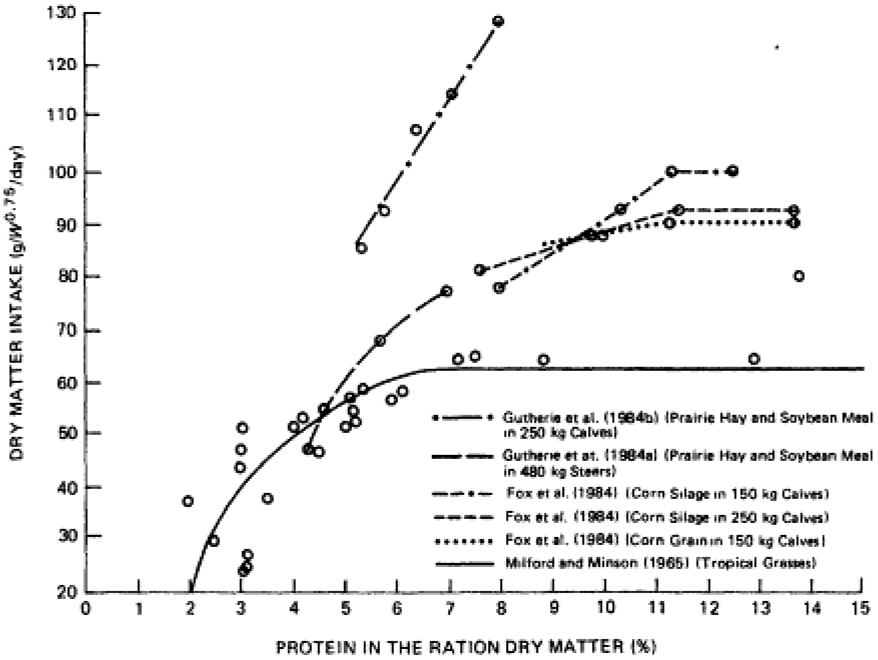

Figure 6-7
Influence of diet type and protein level on dry matter intake.

AN EVALUATION OF ALTERNATIVE SYSTEMS FOR PREDICTING INTAKE BY BEEF CATTLE

A number of systems for predicting intake of beef cattle based on summaries of different data bases have been published recently. Each may be useful under different conditions, when the limitations are taken into account or when they are not applicable. The published equations and factors for each and a summary of likely limitations based on the previous discussion are given.

1. *NRC (1984)*. The data base is published information from various studies. DMI (kg/day) = $W^{0.75}$ $(0.1493\text{NE}_m - 0.046\text{NE}_m{}^2 - 0.0196)$, where DMI is dry matter intake; add 10 percent for large-frame steer calves and medium-frame yearling steers; add 5 percent for large-frame bulls; subtract 10 percent for medium-frame heifers.

Limitations

a. Needs more refined adjustment for frame size and sex.
b. Needs adjustment for stage of growth.
c. Needs adjustments for feed additives, dairy breed type, and environment.
d. Needs adjustment for diet processing.

2. *Plegge et al. (1984)*. Data base is a summary of feeding trials conducted in Minnesota between 1966 and 1984, including 617 pens (14,199 cattle); cattle were fed mostly under sheltered conditions. All of these were used to develop an intake equation based on mean weights and intake during the feeding period. Cattle in 158 of the pens (5,244 cattle) were used to develop an intake equation based on intake and weights for each 28-or 42-day period during the trials.

a. Intake at a particular weight (kg/day) = $-43.18 - 0.004(\text{IW}) + 0.00003(\text{IW}^2) + 36.8326(\text{RW}) - 20.8356(\text{RW})^2 + 24.5011(\text{ME}) - 4.4019(\text{ME}^2)$, where IW is initial weight (in kg), RW is the proportion of finished weight (assumed to be low choice grade), and ME is diet metabolizable energy concentration (in Mcal/kg); $r^2 = 0.80$.
b. Intake based on overall average weight and intake (kg/day) = $-7.65 + 0.0063(\text{AW}) + 0.0000189(\text{AW}^2) + 9.4106(\text{ME}) - 1.9011(\text{ME}^2)$, where AW is the overall average weight from start to finish, and ME is the same as in a above ($r^2 = 0.78$). The adjustments in Table 6-1 need to be applied to the value from the equation in a or b.

Limitations

a. May underestimate feed intake for cattle that have low initial weights for their frame size or may overestimate feed intake of cattle that have high initial weights for their frame size.
b. Does not appear to be applicable to cattle under 250 kg initial weight, especially weaned calves fed high-forage diets.
c. May overestimate the effect of growth stimulants.
d. Need to apply environmental adjustments appropriate for the region.
e. Not clear whether heifer effect is the result of differences in final body fat or a unique sex effect. f. Need adjustment for diet processing.

3. *Owens and Gill (1982)*. Data base is a summary of 15 feeding trials (about 1,500 cattle) at Oklahoma State University, Stillwater, with weights and intakes taken at 28- or 56-day intervals. DMI (kg/day) = $-5.08 + 0.0636W - 0.000072(W^2) + 0.0039\ (\text{IW} - 276.7)$.

Limitations

a. Need to adjust for diet energy concentration.
b. Need to adjust for differences in frame size.
c. Need to adjust for feed additives and environmental conditions.

TABLE 6-1 Adjustments for Sex, Age, Breed, Feed Additive, Growth Stimulants, and Seasons for Plegge et al. (1984)

	Adjustments (kg/day) for:					
Weight	Heifers	Steers	Calves	Yearlings	Beef	Holstein
Particular =	-0.255	0.255	-0.055	0.055	-0.310	0.310
Overall =	-0.185	0.185	-0.205	0.205	-0.265	0.265
	Monesin		Growth Stimulants		Summer	Winter
	With	Without	Without	With		
Particular =	-0.165	0.165	-0.300	0.300	-0.450	0.450
Overall =	-0.185	0.185	-0.295	0.295	-0.145	0.145

d. May not apply to calves weighing under 250 kg fed a high-forage diet.
e. Needs adjustment for diet processing.

4. *Thornton et al. (1985) and Owens et al. (1985)*. Data base is 675 pens (total of 119,482 head) of yearling steers of English breeding, implanted with a growth stimulant, fed an ionophore-supplemented high-concentrate diet in a large unsheltered feedlot in western Kansas from December 1981 through November 1982.

a. Adaptation (first 14 days): DM intake (kg/day) = $0.0217\ W^{1.02}$; $r^2 = 0.54$.
b. After 14 days: DM intake (kg/day) = 6.93 + 0.019 (days on feed) - 0.00013 (days on feed2) + 0.0000248 IW^2; $r^2 = 0.38$.
c. Mean DM intake over 112 days on feed (kg/day) = $0.197W^{0.656}$; $r^2 = 0.54$.
d. Adjustments, based on 48 pens of heifers (5,012 head) and 22 pens of Holsteins (2,056 head): heifers, none; Holsteins, 10 percent.

Limitations

a. Does not adjust for variations in diet energy concentration.
b. Does not adjust for nonuse of ionophores and growth stimulants.
c. May not apply to calves since the data base was yearlings.
d. Diet-processing effects not considered.
e. Environmental effects not considered.
f. r^2 values were low.

5. *Fox and Black (1984)*. Data base is information from feeding trials reported in various sources, primarily experiment station bulletins and research reports.

DMI (kg/day) = $0.1\ W^{0.75}$ for average-frame-size steer equivalent weight of 364 kg and then decreased by 2 g/$W^{0.75}$ for each additional 22 kg. Base intake decreased 2 g/$W^{0.75}$ for each 0.02-Mcal/kg increase in diet NE_m above 1.27 Mcal/kg. There was an intake increase of 10 percent for yearlings and 17 percent for Holsteins and a decrease of 10 percent for monensin and 2 percent for lasalocid. There was an intake decrease of 35 percent for temperatures > 35°C if no night cooling and 10 percent for temperatures > 35°C with night cooling, or 25-35°C; there was an intake increase of 3, 5, 7, and 16 percent as temperature fell from 5 to -5°C, 15 to 5°C, - 5 to - 15°C, and below - 15°C, respectively. Intake was decreased by 15 percent for mild mud and 30 percent for severe mud.

Limitations

a. Not applicable to diets of less than 1.54 Mcal NE*m*/kg.
b. More refined adjustment is needed for age (initial weight).
c. Overestimates intake of young Holstein steers, especially above 22 percent body fat.
d. Need to extend adjustment for heavier than low choice grade.
e. Needs adjustment for diet processing.

6. *ARC (1980)*. Data base is a summary of data reported in six journals. DMI (kg/day) = $W^{0.75}$ (0.1168 -0.01059 ME), where ME is in Mcal/kg.

Limitations

Data are not refined enough. No adjustments are given for any of the effects identified previously, except diet energy density.

7. *NRC (1984), for breeding females*. Data base is information taken from various drylot feeding trials with beef cows, primarily reported in experiment station bulletins and research reports. DMI (kg/day) = $W^{0.75}$ ($0.1462NE_m$ - $0.0517NE_m2$ - 0.0074).

Limitations

a. Not clear why intake for breeding females should be higher at low energy densities and lower at high-energy densities than that for growing and finishing cattle.
b. Needs adjustment for level of milk production.
c. Needs adjustment for pregnancy.

8. *Fox (NRC, 1987)*. Data base from Vona et al. (1984) includes 16 hays (cultivars of switchgrass, big bluestem, and tall fescue) collected in five states (Iowa, Kentucky, New Jersey, New York, and Pennsylvania) at three stages of growth (vegetative, early head, and early bloom). DMI (kg/day) = $W^{0.75}$ (19.4 + 54.5 NE_m); $r^2 = .64$. In developing this equation, a linear equation was as closely related to intake as a nonlinear one. This indicates that over the range of forage energy densities usually fed to beef cows, a linear equation adequately describes intake.

Limitations

a. Needs adjustment for level of milk production.
b. Needs adjustment for pregnancy.

SUMMARY OF FACTORS INFLUENCING INTAKE OF BEEF CATTLE

This section summarizes the factors influencing intake of beef cattle, based on the review presented in this chapter. Users of this information may choose to use some combination of systems 1-5 presented in the preceding section and the factors presented here.

TABLE 6-2 Adjustment of Actual Weight to Average Frame Equivalent Weight

	Adjustment Factors for the Following Frame Sizes								
Sex	1	2	3	4	5	6	7	8	9
Steers	1.25	1.19	1.13	1.06	1.00	0.95	0.92	0.87	0.83
Heifers	1.56	1.47	1.39	1.32	1.25	1.19	1.14	1.09	1.04
Bulls	1.04	0.98	0.93	0.88	0.83	0.79	0.76	0.73	0.69

1. Diet energy concentration: NRC (1984) and Plegge et al. (1984) equations for growing cattle and Fox (NRC, 1987) equations for beef cows given in previous section.
2. Body fat (Fox and Black, 1984).

Relative intake of beef cows may decline above a condition score of 5 (1 = extremely thin, 9 = extremely fat), which is a body fat value of 22 percent (George, 1984).

Adjustment factors can be determined for alternative frame sizes of growing cattle by multiplying actual weight by the adjustment factor in Table 6-2 and then by using the adjusted weight (equivalent weight) to get the intake adjustment factor from Table 6-3. Then the adjusted intake/$W^{0.75}$ is applied to the animal's actual weight to predict kg of DM/day. For example, a frame size 9 steer weighing 500 kg has an equivalent weight of 500 × 0.83 = 415 kg. The appropriate body fat adjustment factor is -3 percent.

3. Initial weight, when placed on finishing diet (Thornton et al., 1985; Gill, personal communication, 1985): 1.5 kg/100 kg increase in initial weight above 225 kg.
4. Unique breed effects (Fox and Black, 1984; Plegge et al., 1984; Owens et al., 1985).

All beef breeds: none
Holsteins continuously on high-energy diet after 8 to 12 weeks of age: none.
Other Holsteins: 8 percent

5. Genetic variance (D. G. Fox, Cornell University, unpublished data, 1983).
   High selection pressure for relative growth rate: 12 percent.
6. Nonuse of an anabolic stimulant (Plegge et al., 1984): -8 percent.

TABLE 6-3 Adjustment for Body Fat

Average Frame Steer Equivalent Weight (kg)	Empty Body Fat (%)	Intake Adjustment
≤ 350	21.3	None
400	23.8	-3%
450	26.5	-10%
500	29.0	-18%
550	31.5	-27%

TABLE 6-4 Adjustment for Finely Processed Diets

Diet NE_m (Mcal/kg)	Adjustment (%)
1.00	47
1.35	20
1.70	None
2.05	-17

7. Feed additives (Fox and Black, 1984):

Additive	Adjustment factor (%)
Monensin @ 33g/1,000 kg of diet	- 10
Monensin @ 22g/1,000 kg of diet	- 6
Lasalocid in diet	- 2

8. Finely processed diet (ARC, 1980) (Table 6-4).
9. Environmental factors (NRC, 1981) (Table 6-5).
10. Forage availability for grazing cattle (Rayburn, 1986).

Rotational grazing: Relative DMI (%) = 103-(710/ DFA), where DFA is daily forage allowance in g of organic matter/kg of live weight (r^2 = 0.86; standard error [SE] = 1.8). Continuous grazing: Relative DMI (%) = 94-(13,500/ FSC), where FSC is kg of forage standing crop/ha (r^2 = 0.54; SE = 6.5).

11. Milk production (George, 1984; ARC, 1980) (Table 6-6).
12. Forage intake of nursing calves. Fox (NRC, 1986) based on LeDu et al. (1976). (Table 6-7).

TABLE 6-5 Adjustment for Environmental Conditions

Temperature (°C) or Lot Condition	Intake Adjustment[a] (%)
> 35, with no night cooling	- 35
> 35, with night cooling	- 10
25 to 35	- 10
15 to 25	None
5 to 15	3
-5 to 5	5
-15 to -5	7
<< -15	16
Mild mud (10 to 20 cm)	- 15
Severe mud (30 to 60 cm)	-30

[a] Adjustments assume that cattle are not exposed to wind and storms.

TABLE 6-6 Adjustment for Milk Production of Beef Cows

Breed	Range in Milk Production First 60 Days Postpartum (kg/day)	Increased Intake (kg/day)[a]
Angus	3-9	0.6-1.8
Brahman	2-6	0.4-1.2
Charolais	3-8	0.6-1.6
Chianina	2-9	0.4-1.8
Hereford	3-8	0.6-1.6
Limousin	2-6	0.4-1.2
Salers	3-9	0.6-1.8
Shorthorn	6-17	1.2-3.4
Simmental	6-17	1.2-3.4
South Devon	3-9	0.2-1.8

[a] 0.2 kg/kg of milk produced (ARC, 1980).

SOURCE: George, 1984; ARC, 1980.

Based on forage dry matter that is 81.9 percent and milk dry matter that is 92.9 percent organic matter, respectively.

13. Pregnancy (ARC, 1980).
    Minus 2 percent per week during the last month.
14. Water intake (Winchester and Morris, 1956) (Table 6-8).

TABLE 6-7 Forage Intake of Nursing Calves

	Month of Lactation						
	1	2	3	4	5	6	7
Intercept	35.6	26.7	24.1	17.9	22.8	22.4	22.4
Slope	-3.11	-2.12	-2.19	-1.71	-2.21	-2.60	-2.60

NOTE: *y* = g of forage organic matter grazed/kg of live weight, and *x* = milk organic matter intake/kg of live weight.

TABLE 6-8 Expected Percentage of Water in Total Daily Intake of Cattle

Environmental temperatures (C°)					
To 4	10	16	21	27	32
74.7	76.2	78.6	81.2	83.2	87.6

NOTE: Add 0.87 kg of water to total intake for each kg of milk produced. Water intake = (dry matter intake/percentage of water in intake) - dry matter intake. For example, if dry matter intake = 10 kg, total water intake at 10°C = [10/(1 - 0.762)] - 10 = 32 kg. If the ration contains 50 percent dry matter, then the free water intake =32 -10=22 kg.

APPLICATION OF EQUATIONS AND ADJUSTMENTS

The usefulness of intake predictions depends on the ability to use them to predict rate and cost of gain and to evaluate management practices. To further assess the application of the equations presented, several evaluations were made, as follows.

Yearlings

Average values from the data of Thornton et al. (1985) were used to evaluate the ability of the equations given above to predict the intake and rate of gain by 14-day intervals. Table 6-9 summarizes the results of these calculations. To estimate the average weight for each period, the rate of gain was estimated from the given intakes. Predicted daily gain from actual intake exceeded actual overall gain (1.35 kg/day) by 27 percent, when the calculated diet net energy values given were used. The intakes appeared to exceed three times maintenance for most periods. Owens and Gill (1982) reported a depression of 4.8 percent in diet digestibility per multiple of maintenance intake on a high-concentrate ration. As intake increases above maintenance, this effect is magnified, up to about three times maintenance, at which point the effect plateaus. Van-Soest et al. (1984) developed discount factors to adjust for the intake effect on digestion for various feeds. A value of 4 percent per multiple of maintenance intake was applied to the calculated diet net energy values for use in projecting period gains, using the system of Fox and Black (1984). These adjustments must be made at high intakes to determine the effective diet net energy value, as most NRC net energy values are estimated from total digestible nutrients, which is commonly determined at a feed intake near maintenance (VanSoest et al., 1984). When these adjusted net energy values were used, average daily gain projected from actual intakes was within 5 percent of that actually obtained (1.42 versus 1.35 kg/day). The same calculations with the NRC (1984) energy requirement equations resulted in an overprediction of daily gain (1.35 versus 1.71 and 1.54 kg/day for the yearling and calf equations, respectively). The Fox and Black (1984) system was used for predicting gains to evaluate the various intake equations because of its smaller deviation from actual gain with this data set.

Adjusted energy values and predicted interval weights were then used to predict intake with the various systems summarized previously. Intakes at a particular weight exceeded those predicted by the NRC (1984), Plegge et al. (1984), and Fox and Black (1984) by 21 to 28 percent for days 15 to 42, with the differences between actual and predicted values being reduced as the cattle increased in weight (Figure 6-8). The NRC equation, which is based on overall average weights and intakes, clearly was inappropriate for describing intake at a particular weight. Intake obviously declines as the cattle approach the degree of fatness of the current grade of low choice, yield grade 3. Under the conditions

TABLE 6-9 Evaluation of Methods for Predicting Intake of Yearling Steers

Day	Actual DMI (kg)	Estimated Weight (kg)	Energy Discount[c] (%)	Gain Profile[d] (kg/day)	Preducted Daily Intake[a] (kg/day)				Predicted Daily Gain[b] (kg/day)			
					NRC (1984)	Thornton et al. (1985)	Plegge et al. (1984)	Fox and Black (1984)	NRC (1984)	Thornton et al. (1985)	Plegge et al. (1984)	Fox and Black (1984)
0-14	7.91±1.36	321	8.0	1.33	7.97	7.82	7.72	7.58	1.53	1.50	1.47	1.44
15-28	9.91±1.23	329	10.4	1.72	8.20	9.69	7.91	7.72	1.55	1.90	1.48	1.44
29-42	9.95±0.95	352	9.6	1.64	8.50	9.85	8.28	8.12	1.54	1.83	1.47	1.44
43-56	10.04 ±0.91	374	9.2	1.57	8.95	9.96	8.56	8.50	1.54	1.76	1.45	1.44
57-70	10.13 ±0.91	394	8.8	1.52	9.28	10.03	8.74	8.58	1.53	1.69	1.41	1.38
71-84	10.18 ±0.95	415	8.4	1.46	9.62	10.04	8.86	8.74	1.53	1.61	1.39	1.34
85-98	10.13 ±0.95	433	8.0	1.40	9.90	10.00	8.90	8.83	1.52	1.54	1.32	1.30
99-112	9.95±0.86	451	7.6	1.32	10.17	9.91	8.80	8.91	1.51	1.46	1.26	1.26
113-126	9.50±0.73	468	6.8	1.29	10.39	9.76	8.79	8.88	1.50	1.38	1.19	1.21
127-140	8.95±0.73	485	6.0	1.07	10.59	9.57	8.65	8.93	1.48	1.29	1.11	1.17
Average	9.67	402	8.3	1.43	9.36	9.66	8.52	8.48	1.52	1.60	1.36	1.34

NOTE: Based on the data of Thornton et al. (1985); intakes are averages for 14-day periods by 119,482 yearling British breed cattle over a 12-month period with an average initial weight of 312 ± 36 kg and an average daily gain of 1.35 kg/day. The diet was calculated to contain 3.18 Mcal ME/kg DM, 2.18 Mcal NE_m/kg, and 1.39 Mcal NE_g/kg DM.

[a] Discounted diet net energy values are used, resulting in the assumption that this is the effective value that will influence the chemostatic intake control mechanism.

[b] Using the system of Fox and Black (1984) and the intakes predicted by each system using computed diet net energy values.

[c] Based on Van Soest et al. (1984); maintenance intake is based on required NE_m of 77 kcal/$W^{0.75}$ and diet NE_m of 2.18 Mcal/kg; discount factor = 4%/unit of intake above maintenance. For example, at 321 kg, Mcal/day for maintenance = 5.85; thus, maintenance intake is 5.85/2.18 = 2.68) kg/day. Units of intake above maintenance = (7.91 - 2.68)/2.68 = 1.95.

[d] Predicted from period intake with the system of Fox and Black (1984) using discounted diet net energy values. Mean period weights are estimated from the daily gain of the previous period. Overall predicted daily gain is 1.42 kg/day, compared to an actual value of 1.35 kg/day. Predicted average daily gain with NRC (1984) yearling and calf equations is 1.71 and 1.54, respectively.

of this feedlot, which is probably typical of most high plains commercial feedlots in the United States, yearling cattle appear to reach near maximum intake by 28 to 42 days on feed, which then plateaus until they are near finished (28 percent fat, low choice grade) weight, at which time intake begins to decline rapidly. Thornton et al. (1985) concluded that under these conditions intake patterns were usually established by 28 days on feed and can be used along with initial weight and days on feed to predict intake beyond that point (Figure 6-9). However, variability was large as evidenced by r^2 values of 0.30 to 0.47, even though the data were restricted to

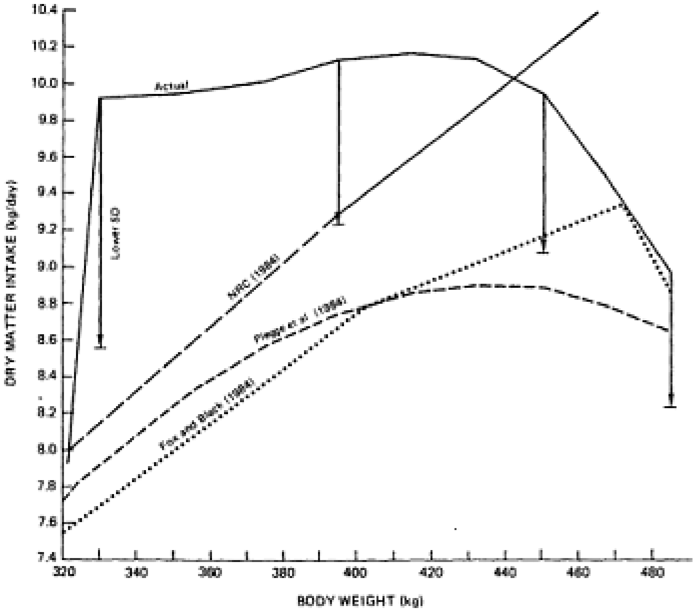

Figure 6-8
Predicted intake of yearling steers. SD, standard deviation.

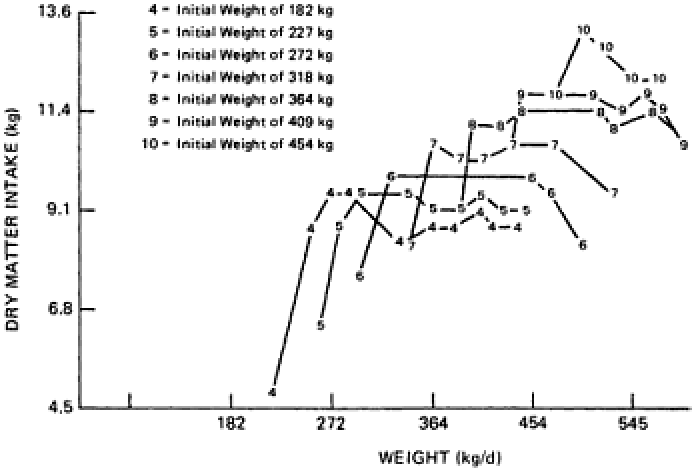

Figure 6-9
Intake versus initial weight. Source: Thornton et al. (1985).

yearling steers of British breeding. It is apparent that variations in frame size, previous nutritional treatment, selection practices, and other factors yet to be identified are involved. It is not clear why the other systems grossly underpredicted intake from 28 to 84 days on feed and to a lesser degree at heavier weights. It may likely be related to the fact that their data are based on experimental conditions such as a smaller pen size, cattle were usually fed in confinement, there was less genetic variation (as evidenced by an r^2 of 0.78), and a smaller proportion of cattle came from backgrounds known to increase intake, such as wheat pasture and thin body condition.

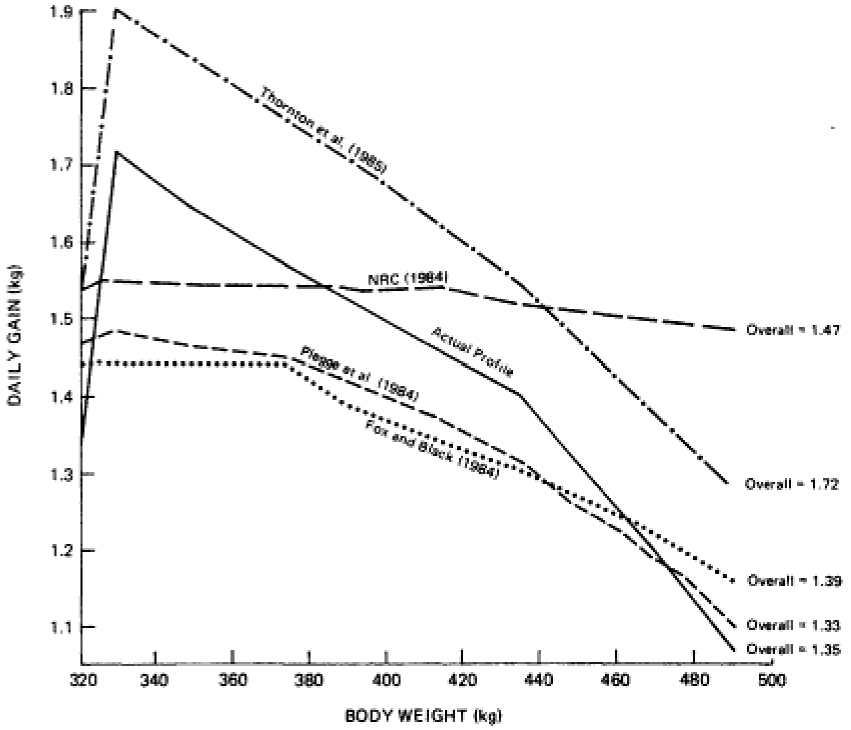

Figure 6-10

Predicted gain without discounting diet NE.

When the equations for mean intake were used, the predicted intake values were much closer to actual intake values (Table 6-9). These results indicate that most of the mean intake equations can be used to predict overall performance whenever expected intake for the feedlot is not known, with the period equations being useful primarily to determine if the cattle are consuming more or less than that which is expected, for use in making daily management decisions.

The usefulness of each equation in predicting weight gains and feeding efficiency was examined, assuming that actual intakes were not known. The results of this evaluation are summarized in Table 6-9 and Figure 6-10. The equation of Thornton et al. (1985) resulted in an overprediction of the rate of gain. Except for that of NRC (1984), the other systems predicted the rate of gain because the lower predicted intake was associated with higher feed net energy values. However, all of the systems overpredicted feed efficiency because of a lower predicted intake to achieve the same rate of gain.

Calves

Data were obtained that included a wide variation in initial weights, frame sizes, and diet net energy values to evaluate the equations presented for predicting feed intake of calves. The data were selected to include most of the extremes in frame sizes and diet net energy values normally experienced under field conditions. A second condition was to have body composition data to allow for an accurate description of frame size and relative weight to apply the various equations and adjustments, and dry matter intakes were available by 28-day intervals; actual diet net energy values were also available. Two data sets were obtained. The first represented three experiments conducted at the Pennsylvania State University, University Park (courtesy H. W. Harpster, Pennsylvania State University, personal communication, 1983; and data from studies of Wahlburg [1981] and Loy [1983]); included were 207 pen observations. The second represented four experiments conducted at Michigan State University, East Lansing (data of Woody [1978] and Harpster [1978]); included were 371 pen observations.

A summary of the evaluations conducted are pre sented in Table 6-10. The NRC (1984) equation averaged within 4 to 7 percent of actual intake ($r^2 = 0.83$), and the Fox and Black (1984) equation averaged within 2 percent of actual intake ($r^2 = 0.86$). It appears that both of these adequately describe average intake, but the Fox and Black (1984) equation was more accurate at a particular weight because of the adjustment for stage of growth. This is of importance when simulating cost of gain to incremental final weights to identify the most profitable sale weight. The equation of Plegge et al. (1984) underestimated intake by an average of 13 to 18 percent ($r^2 = 0.66$), which appeared to be an effect of the initial weight function. Further work is needed to determine the reasons why, under some conditions, initial weight is an important factor. Differences in frame size, protein nutrition, and environmental conditions are possibilities.

Predicted versus actual daily gains were determined with the Michigan data, using the NRC (1984) equations for the various frame sizes and sexes and the equation of Fox and Black (1984). Daily gains were based on weight adjusted to a constant dressing percentage; all were fed to a similar level of empty body fat (28.1 percent). Actual daily gain averaged 1.06 kg/day; daily gain predicted from actual intakes by the NRC (1984) and Fox and Black (1984) equations averaged 1.06 and 0.98 kg/ day, respectively, over a range of actual daily gains from 0.75 to 1.47 kg/day. In an evaluation with seven pens of calves (474 head) in a commercial feedlot in Florida, the Fox and Black (1984) equation predicted daily gain within I percent with steers and 3 percent with heifers, using actual intakes. Thus under research conditions the NRC (1984) equations were very accurate in predicting overall daily gain, but the Fox and Black equation was more accurate in both yearling and calf commercial feedlot evaluations. Rouse and Loy (Iowa State University, personal communication, 1985) found that the NRC equations overpredicted daily gain of small- and average-frame-size cattle in commercial feedlots in Iowa but was accurate on large frame-sized cattle. Both the Fox and Black and NRC equations use the same maintenance requirement; the NRC system has a lower gain requirement. Since the NRC gain equations appear to be more accurate under research conditions, it is implied that maintenance requirements are typically higher under commercial feedlot conditions. This is likely due to the elimination of the start-up period and sick and low-performing cattle under research conditions, and in some cases the fact that cattle were fed in a less stressful environment.

These evaluations indicate that adjustments to net energy values for level of intake and appropriate energy requirement equations must be used along with the best dry matter intake prediction equations to accurately predict the performance of growing cattle.

Beef Cows

Two data sets were used to evaluate the usefulness of the NRC (1984) equations for predicting intake of dry and lactating beef cows. Fox (NRC, 1987) developed the first data set from Vona et al. (1984) in which dry beef cows (Angus, Hereford, and Charolais crossbreeds) were used to determine the intake and digestibility of warm-season grasses (fed in the long form) over a period of 2 years at different stages of growth across the eastern and central United States. (See Item 8 in the section entitled "An Evaluation of Alternative Systems for Predicting Intake by Beef Cattle.") The data base included 16 grass hays (cultivars of switchgrass, big bluestem, and tall rescue) harvested in five states at three stages of growth (vegetative, early head, and early bloom). The results are presented in Figure 6-11. Intake was lower than that predicted by either equation at lower energy densities (late-cut hay) and was higher than that predicted at higher energy densities (vegetative stage, which is typical of well-managed pastures); r^2 values for the NRC (1984) growing cattle and NRC beef cattle equations were 0.65 and 0.47, respectively. These data covered the range in qualities of forages usually fed to beef cows, a number of forages and locations were included, and intake and energy values were determined under standardized conditions.

The data of Holloway and Butts (1983) was used to evaluate the adequacy of Fox (NRC, 1987) and NRC (1984) equations to predict the intake of grazing beef

TABLE 6-10 Evaluation of Dry Matter Intake Prediction for Calves

Data Source	Initial Weight (kg)	Final Weight (kg)	Frame Size[a]	Diet NE_m (Mcal/kg)	Diet NE_g (Mcal/kg)	Actual Dry Matter Intake (kg/ day)	Predicted Dry Matter Intake (kg/day)		
							NRC (1984)	Plegge et al. (1984)	Fox and Black (1984)
Pennsylvania studies[b]	241-284	454-545	4-7	1.50-1.82	0.99-1.39	8.18	8.51	7.27	8.31
Michigan studies[c]	135-275	356-578	3-8	1.50-2.05	0.95-1.52	7.72	8.27	6.35	7.88

[a] Based on actual final body composition and the system of Fox and Black (1984).

[b] Includes 207 pen observations taken at 28-day intervals (Walburg, 1981; Loy, 1983).

[c] Includes 371 pen observations taken at 28-day intervals (Woody, 1978; Harpster, 1978).

cows nursing calves. This data base was collected from studies on Angus cows grazing fescue-legume pastures over a period of 5 years. The stocking rate was 0.81 ha/ cow-calf pair, with a weekly rotation between two pastures per treatment group. Legumes and fertilizer were added each year to keep forage availability high; nursing calf weights averaged 273 kg after 150 days of grazing, indicating that forage availability was not limiting. The results of this evaluation are presented in Figure 6-12. The Fox (NRC, 1987) equation was within 4 percent of actual intake at the highest energy density and was within 6 percent at the lowest energy density, was similar at the middle energy density, and averaged within 3 percent overall. The NRC (1984) equations were more variable (Figure 6-12). This evaluation suggests that when forage availability is not limiting, the equation given above can be used to estimate the intake of grazing beef cows with nursing calves.

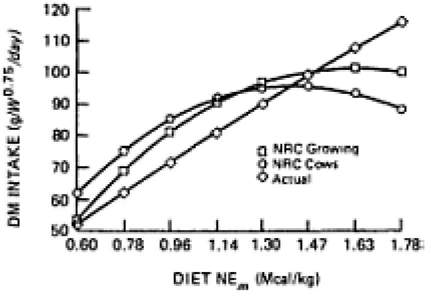

Figure 6-11 Dry matter intake of dry beef cows. The equation for actual values was developed from Vona et al. (1984); DMI = $W^{0.75}$ (19.4 + 54.5 NE_m) $r^2 = 0.64$. The data base includes 16 hays (cultivars of switchgrass, big bluestem, and tall fescue) collected in five states (Iowa, Kentucky, New Jersey, New York, and Pennsylvania) at three stages of growth (vegetative, early head, and early bloom).

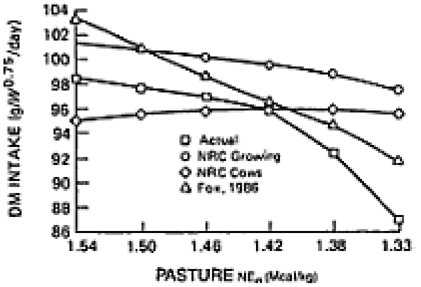

Figure 6-12 Dry matter intake of grazing beef cows nursing calves. Actual data are those of Holloway and Butts (1983); includes 90 cow years collected over 5 years of grazing fescue-legume pastures (10 cows with calves on 8.1-ha pastures, rotated weekly), from the second 30 days of lactation (6.2 kg of milk/day, 151-kg calves) to the last 30 days of lactation (3.5 kg of milk/day, 273-kg calves). U.S. Department of Agriculture.

The addition of the adjustments given for milk production would have added 13 percent to intake during early lactation, declining to an additional 8 percent by late lactation. It is not clear under what conditions this adjustment should be made; predicted intake plus this factor could represent the difference between grazing and drylot intakes.

In the studies evaluated here, nursing calf forage intakes/$W^{0.75}$ were 67 g at 175 kg, 93 g at 199 kg, and 108 g at 248 kg body weight; intakes were not taken at lighter weights. Total intake of forage and milk at these same weights were 81, 104, and 115 g/$W^{0.75}$, respectively, with actual/predicted ratios of 0.98, 1.20, and 1.15.

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7

Sheep

INTRODUCTION

Like beef cattle, sheep are raised primarily as a means of marketing forages, especially those forages that have limited alternative markets. It is important to predict intake to determine the proportion of their nutrient requirements that can be met from forages, so that the amount of supplemental nutrients needed can be estimated. In sheep feed intake is controlled by physiological demand due to maintenance needs and production demands, up to the limits of gastrointestinal (GI) capacity (Mertens, 1973). Usually GI capacity is adequate for dry ewes to nearly meet their requirements from low-quality forages, especially until the last 30 days before lambing. GI capacity also allows lactating ewes to meet their own requirements for maintenance and lactation and to meet the requirements of their nursing lambs for near maximum growth when the diet is high-quality forage and the quantity available is not limiting (K. E. McClure, C. F. Parker, and S. C. Loerch, Ohio Agricultural Research and Development Center, personal communication, 1985). Intake of weaned lambs that are finished in drylot, however, is limited primarily by the demand for maximum growth potential as well as dietary factors in addition to GI fill. Nutrient requirements are related to rate of production, which depends primarily on the intake of the diet being fed (National Research Council [NRC], 1975). Therefore, under most conditions intake must be predicted before diets can be formulated to meet nutrient requirements, unless they are limit-fed a high-nutrient-density diet that would exceed their requirements if fed to appetite. This is not the usual case; management problems such as wool eating often occur under these conditions (McClure et al., personal communication, 1985). When sheep are fed to appetite and intake is accurately predicted, nutrient requirements can be expressed as a percentage of the diet, which also most appropriately expresses requirements for rumen fermentation (Fox et al., 1984).

The purpose of this chapter is to identify and discuss the primary factors influencing feed intake in sheep and to present equations and adjustment factors that can be used to predict feed intake of sheep under widely varying feeding and environmental conditions.

PHYSIOLOGICAL AND DIETARY FACTORS

Many of the same fundamental factors that influence feed intake of cattle, as described in Chapter 6 for beef cattle, apply also to sheep. An extensive review by the Agricultural Research Council (ARC; 1980) revealed that for finely processed diets intake/$W^{0.75}$ (relative intake, where W is live weight) was 90.5 g for sheep versus 89.5 g for cattle. These values were derived from a summary of data reported in six journals. Average diet dry matter (DM) energy values (Mcal of NE_m/kg, where NE_m is net energy for maintenance) were 1.45 for sheep and 1.64 for cattle; both values are within the range of dietary energy values at which intake is maximum, as shown in Chapter 6 for beef cattle. Within this range of energy values, the NRC (1975) suggests intake of growing sheep is 103 g/$W^{0.75}$, based on the data of Rattray et al. (1973) in which pelleted diets were fed to sheep. Figure 7-1 shows the relationship of intake to stage of growth, comparing the values reported by the ARC (1980) and that given in Chapter 6 for cattle at approximately the same degree of body fatness. At the same stage of growth, intakes appear to be similar for cattle and sheep, when milled and/or pelleted diets are fed. Thus, as with cattle, cell wall content (neutral detergent fiber, NDF) of the diet is the primary factor limiting intake, unless high-concentrate diets are being fed. In creasing dietary concentration of slowly degraded or indigestible material reduces the rate of passage and physical fill becomes limiting (Mertens and Ely, 1982; VanSoest, 1982; Mertens, 1983). As digestible energy content is increased, for example, when grain in the diet is increased, metabolic controls become the dominant factors limiting intake. The use of diet energy concentration to predict intake describes the combined effects of physical fill and metabolic controls on appetite.

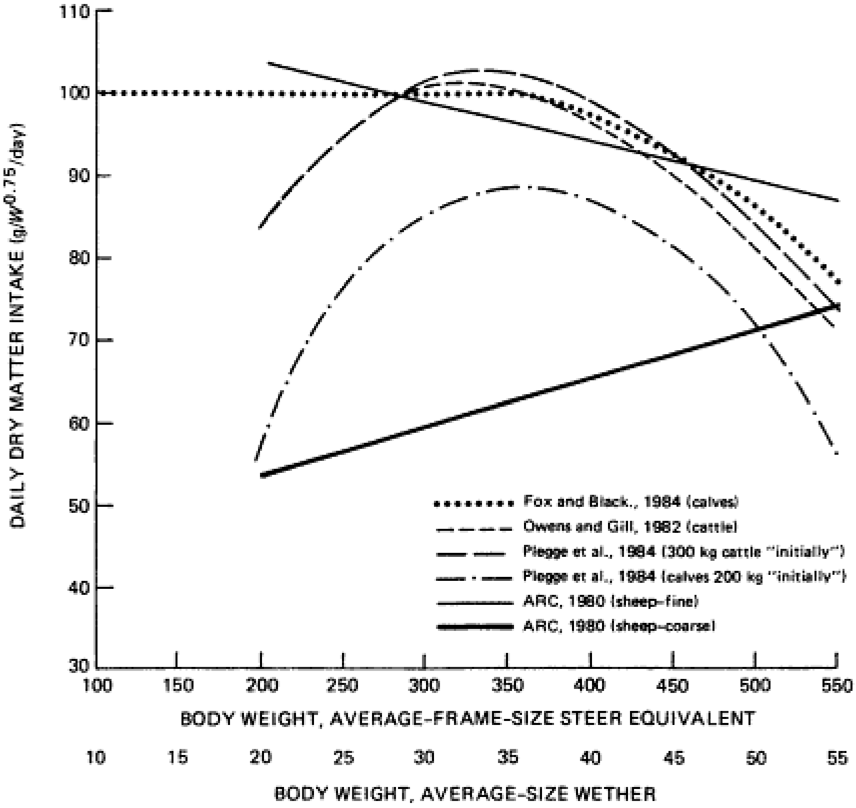

Figure 7-1
Relationship of stage of growth to intake in sheep.

There appears to be some unique differences between cattle and sheep when fed long or chopped roughages or silages. ARC (1980) found that dry matter intake was similar (87 versus 90 $g/W^{0\ 75}$) for cattle when fed coarse (long or chopped) versus fine (milled and/or pelleted) forage at high energy densities. However, long or coarsely chopped forage gave relative intakes in sheep of 57 $g/W^{0.75}$ as compared to 90.5 g for fine diets; silages gave 46 $g/W^{0.75}$. Average diet energy densities (Mcal of NE_m/kg of DM)were 1.39, 1.45, and 1.50, respectively; all are within the range over which diet energy density would not be expected to influence intake. Similar results for roughages (441 determinations of ad libitum forage intake across 2,747 individual animal intakes) were reported by Heaney et al. (1968); chopped mixed hay gave 66 $g/W^{0.75}$, while the same hay in pelleted form gave 135 $g/W^{0.75}$. Silage intake averaged 54 g. The overall coefficient of variation was 16.4 percent; within and between animal variation was high. Demarquilly (1973) found silage intake to be 47 g across 87 silages, a value 33 percent lower than the intake from the same herbages prior to ensiling.

Intake of silage by sheep is not closely related to its digestibility but is more closely related to its fermentation characteristics (Demarquilly, 1973; Wilkins, 1974). Wilkins (1974) concluded that the depression in intake after fermentation appeared to be due primarily to the increased total volatile fatty acids (VFAs). Part of the differences in the literature are due to the effect of oven drying on loss of VFAs (Fox and Fenderson, 1978). Most of the intake differences between fermented and unfermented forage when fed to cattle are due to this effect. However, the large intake depression in sheep observed from feeding fermented feeds is apparently due to physiological effects. In Chapter 1, it was stated that receptors in the sheep's duodenum are particularly sensitive to the duodenal concentration of lactic acid. Thus, silages that tend to be high in lactic acid (immature or treated with products that extend fermentation) would be expected to depress intake more than those that are low in lactic acid (more mature, not treated with fermentation extenders). In the studies of Johnson and McClure (1968), where corn silages were compared when harvested from the blister (21 percent DM) to the mature (72 percent DM) stages, intakes averaged 54 g/$W^{0.75}$, a value comparable to those cited previously. Intake was as much as 20 percent lower at the blister and milk stages, however, where lactic acid content averaged 12.8 percent compared to 8.4 percent overall. Another key factor in feeding silages to sheep may be the distribution of nitrogen in silage and the nitrogen supplementation used. In these studies, nonprotein nitrogen (NPN) was used for nitrogen supplementation; protein solubility is usually 60 to 70 percent in NPN-supplemented corn silage (Lomas et al., 1982) and would likely exceed 70 percent in immature silages. However, intakes of 93 g/$W^{0.75}$ on a corn silage diet supplemented with soybean meal were achieved in growing lambs (McClure et al., personal communication, 1985).

It may be that the sheep's reticulum possesses stretch receptors that are sensitive to distension of the gut after a meal. This factor, when coupled with the longer lag time before digestion begins, slower rate of digestion, and longer retention time of long versus chopped forages, may explain the unique effect of length of forage on intake in sheep. Mertens and Ely (1982) concluded that cattle digest feeds with low digestibilities to a greater extent than do sheep.

Lactation also influences feed intake of sheep. An excellent summary on that effect is presented by ARC (1980). As with cattle, ewes increase intake as lactation progresses to the fourth week; intake then begins to decline by the seventh week of lactation. They are further influenced by the number of lambs they are nursing. Intake averages are approximately one-third higher when ewes are nursing one lamb and one-half higher when nursing two lambs.

PREDICTING DRY MATTER INTAKE OF SHEEP

Based on the information presented in Chapter 1, the biological factors that appear to control intake are those related directly to direct dietary effects (distension of body wall, ruminal pH and acetate concentration, hepatic uptake of propionate) and metabolic factors mediated by the central nervous system, including size of adipose mass and demand for nutrients.

The equation that best represents the biological effect is one that primarily reflects the influence of fill or distension with feeds with slow rates of digestibility and passage, and the influence of amounts of end products of digestion that result when rates of digestibility and passage are expected to be high. Adjustments are then made for size of adipose mass and demand for energy (level of production and climatic effects). Such a prediction function should be continuous, because most biological responses are continuous rather than point effects, and it can be used over a wide range of conditions.

Equations and adjustments suggested in this section are illustrated in Figure 7-2. They were selected from a variety of sources, since it would be next to impossible to identify all of the independent variables from any one data base. The concentration of NE_m was selected as the independent variable, since it represents the widest combination of dietary and animal production conditions. Even with the best equations and adjustments, however, intake may vary from predicted values by 10 percent or more.

The data of Mertens (1973) were used to derive equations to predict intake of sheep fed forages as follows.

$$\text{g of DMI}/W^{0.75} = 74.4 + 0.877X - 0.017X^2,$$

where X is percent forage cell wall, and DMI is dry matter intake ($r^2 = 0.76$). The range of data was 30 to 80 percent cell wall. This equation was developed from 187 intake and digestibility trials from 12 experiment stations in the United States, the Philippines, and Puerto Rico. All but one trial was with sheep.

The net energy value for lactation (Mertens, 1983; based on Mertens, 1973), Mcal/kg of DM for legumes is

$$\text{NEL} = 2.40 - 0.0232\,(\text{NDF percent}). \qquad (2a)$$

For grasses the NEL is (Mertens, 1983; based on Mertens, 1973)

$$\text{NEL} = 2.86 - 0.0262\,(\text{NDF percent}). \qquad (2b)$$

The NE_m value can then be calculated (Van Soest et al., 1984):

$$\text{NE}_m = 0.78\text{NEL} + 0.31. \qquad (3)$$

The NE_m concentration (Mcal/kg) was then related to dry matter intake to give the following equations for grasses and legumes. These equations allow for adjustment for fill factors, inherent differences between legumes and grasses in rate of passage, and the influence of end products of digestion as forage digestibility increases. At the higher energy densities, immature forages (in most cases pasture) would be represented.

Intake of legumes

$$(\text{g/day}) = W^{0.75}(-70.4 + 182\text{NE}_m - 53.2\text{NE}_m^{\,2}). \qquad (4)$$

Intake of grasses

$$(\text{g/day}) = W^{0.75}(-81.3 + 166\text{NE}_m - 41.2\text{NE}_m^{\,2}). \qquad (5)$$

The previous discussion indicates that a separate base equation is needed to predict intake of ensiled forages. The value for relative intake of 46 g, as suggested by the

ARC (1980) for ensiled immature forages or those treated with products known to increase lactic acid content, may be the best available estimate. However, silage intake by sheep may follow the pattern described by Equation 5 when ensiled at a more mature stage or at a low water content where lactic acid content is likely to be lower or oil meal supplements are used. More research is needed to separate out more clearly the independent effects of these variables.

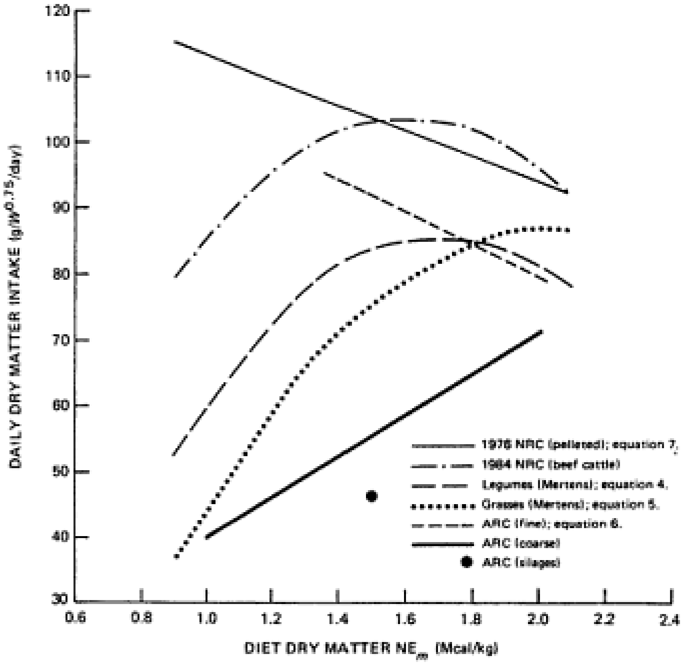

Figure 7-2

Dry matter intake of sheep as related to diet energy density.

As shown in Figure 7-2 and in the previous discussion, it appears that a separate equation is needed to predict intake of pelleted or milled feeds for sheep. Both NRC (1975) and ARC (1980) indicate that the fill factor is overcome by pelleting. At high energy densities, end products of digestion reduce intake. However, at low energy densities the rate of passage becomes the dominant factor; Mertens (1973) found that the rate of passage is more important than the rate of digestion. Both the NRC (1975) and ARC (1980) equations appear to be valid; the NRC equation is based entirely on pelleted diets, while the ARC data base includes both pelleted and finely ground diets. Thus the NRC equation could be used for pelleted diets and the ARC for other finely processed, nonpelleted milled diets.

For intake of milled, nonpelleted diets (ARC, 1980):

$$\text{Intake (g/day)} = W^{0.75}(129 - 22.3\text{NE}_m). \qquad (6)$$

The range of data was 1.35 to 2.05 NE_m/kg of DM. For intake of pelleted diets (NRC, 1975):

$$\text{Intake (g/day)} = W^{0.75}(131 - 18.7\ \text{NE}_m). \qquad (7)$$

The range of data was 0.87 to 1.83 NE_m/kg of DM.

Adjustments are needed for stage of growth; these adjustments represent energy demand for growth, adipose mass, and apparent relative rumen capacity changes with body weight in sheep.

The data of Hogue (1979) and ARC (1980) were used to develop the relationships for stage of growth shown in Table 7-1.

These were then used to develop adjustment factors

TABLE 7-1 Determination of Stage of Growth

Sheep Frame Size	% Body Fat			Breed Types
	21.3	26.5	31.5	
	Equivalent Weights (kg)			
Small	29	36	44	Southdown
Average	36	45	55	Corridale, Dorset
Large	44	55	66	Suffolk

for stage of growth effects based on the ARC (1980) data base, as shown in Table 7-2. The data of ARC (1980) were used to develop the adjustment factors for coarse forages.

TABLE 7-2 Intake Adjustment for Stage of Growth

Lamb Equivalent Weight (kg)	Adjustment (%)	
	Fine Diet	Coarse Diet
20	None	-28
30	None	-20
40	-3	-12
45	-10	-9
50	-18	-6
55	-27	None

As stated in Chapter 1, energy demand is one of the controlling factors of intake. In lactating ewes, as with cattle, intake would be expected to gradually increase with energy demand as lactation progresses and then decline in late lactation. As with cattle, energy demand increases more rapidly than intake early in lactation, but reserves are allowed to be replenished later in lactation when intake exceeds energy demand. Table 7-3 includes intake adjustment factors for lactation based on the ARC (1980) data base.

NRC (1981) reviewed environmental effects on intake. A summary of their findings for sheep are as follows:

1. Exposure to heat reduces voluntary intake in sheep, as it does in other species. Effective ambient temperature, which combines the effects of both temperature and humidity, is the value most closely related to this effect.
2. Voluntary intake increases during exposure to cold relative to the animal's thermal neutral zone (TNZ). However, it reaches a maximum before animals are severely cold stressed.
3. Daily temperature fluctuations around the TNZ did not influence intake. However, more work is needed in this area.

Based on the summary by NRC (1981), temperature adjustment factors were developed (Table 7-4).

These conclusions indicate that adjustments for intake should use as their base the animal's TNZ. Therefore, the relationships in Table 7-4 may need to be shifted as the animal's TNZ changes.

TABLE 7-3 Adjustment for Lactation

No. of Lambs	Adjustment Factor for the Following									
	1	2	3	4	5	6	7	8	9	10
One	1.24	1.27	1.30	1.32	1.33	1.33	1.32	1.31	1.31	1.30
Two	1.40	1.45	1.50	1.53	1.54	1.54	1.53	1.52	1.52	1.51

TABLE 7-4 Adjustment Factors for Temperature

Temperature (°C)	Adjustment Factor[a]
-5	1.10
5	1.05
15	1
25	0.90
35	0.75

[a] Based on TNZ of 15°C and a data base of -5°C to 35°C, with shorn lambs (Brink, 1975). At other TNZs, the adjustment factor relationship may be different.

EVALUATION OF EQUATIONS TO PREDICT INTAKE OF SHEEP

Independent data were obtained to evaluate the equations presented above. Data from feeding trials from the Ohio Agricultural Research and Development Center (K. E. McClure, C. F. Parker, and S. C. Loerch, personal communication, 1985) were summarized and tested against the various equations presented above. Included were diets ranging from corn silage to all concentrate fed to growing lambs and diets ranging from corn stover to high-energy lactation rations fed to ewes during the course of complete reproductive cycles. All were average-frame-size crossbreds, with the lambs in the finishing trials originating from these same ewes. The lamb finishing data were by 14-day intervals, for a total of 129 pen observations with 428 lambs. The ewe data were collected over three complete reproductive cycles at approximately 30-day intervals, for a total of 52 observations with 572 ewes.

Table 7-5 summarizes the comparisons that were made. Lambs fed the all-pelleted diets had intakes nearly identical to that predicted by Equation 7. The silage intake was best predicted by Equation 5, as expected. However, the response was not linear with increases in weight as these equations imply; equations were developed from these data to take into account this effect. Figures 7-3 and 7-4 compare Equations 7 and 5 with those developed from these data, as follows. For intake of pelleted diets fed to lambs:

$$\text{Intake (kg/day)} = -0.414 + 0.303W^{0.75} - 0.00755(W^{0.75})^2 - 0.504\text{NE}_m\ (r^2 = 0.78). \qquad (8)$$

For intake of corn silage supplemented with soybean meal:

$$\text{Intake (kg/day)} = -4.19 + 0.297W^{0.75} - 0.00843(W^{0.75})^2 + 1.77\text{NE}_m\ (r^2 = 0.98). \qquad (9)$$

TABLE 7-5 Evaluation of Equations to Predict Intake of Sheep

Diet[a]	Average Weight (kg)	Average NE_m (Mcal/kg)	Prediction Equation Number				
			Actual	4; Legumes	5; Grass	6; Milled	7; Pelleted
Intake of growing lambs (kg/day)							
Pelleted	33	1.85	1.36	1.14	1.15	1.21	1.33
Silage	31	1.78	1.05	1.06	1.07	1.17	1.28
Intake of ewes (kg/day)[b]							
Overall	62	1.27	1.70	1.78	1.53	2.45	2.62
Early gestation	60	1.03	1.42	1.31	1.00	2.29	2.41
Mid-gestation	61	1.11	1.31	1.42	1.12	2.28	2.41
Late gestation	65	1.42	1.71	1.82	1.61	2.22	2.38
Lactation[c]	61	1.60	2.44	2.73	2.54	3.02	3.27
Maintenance	60	0.90	1.19	1.07	0.74	2.35	2.47

[a] The pelleted diets were whole or pelleted corn based, with alfalfa meal as a roughage.

The silage was whole plant corn silage. All were average-frame-size crossbred ewe and wether lambs from the ewes reported in this table. The data were evaluated by 14-day intervals, giving a total of 129 pen observations with 428 lambs over four experiments. The corn silage data were available in only one of these trials.

[b] Data were collected over three complete reproductive cycles at approximately 30-day intervals, for a total of 129 pen observations with 572 ewe observations.

[c] Adjustment factors were applied from Table 7-3 for the number of lambs nursed, which ranged from 1.3 to 2.5 per ewe across the groups fed over the three reproductive cycles represented.

SOURCE: K. E. McClure, C. F. Parker, and S. C. Loerch, Ohio Agricultural Research and Development Center, personal communication, 1985.

Equation 4 was adequate in predicting the intake of the ewes, and the overall average was within 2 percent of the actual intake. The ewes had been fed to maintain a constant condition score, so their intake met their nutrient requirements when feeds of the energy density shown in Table 7-4 were fed to appetite. Equation 5 consistently underpredicted intake with the low-energy diets. All of these diets were supplemented as needed with soybean meal and minerals to meet nutrient requirements, however.

The data of Vona et al. (1984) were used to evaluate the intake equations presented for predicting intake of hay. These data included 16 hays (cultivars of switch-grass, big bluestem, and tall fescue) harvested in five states across the central and eastern United States at three stages of growth (vegetative, early head, and bloom) over a 2-year period. They were fed to wethers in the chopped form in one location to determine the effect of forage stage of growth on intake and digestibility. Actual intake was compared to that predicted by the intake equations presented previously for legumes and grasses. The results are summarized in Figure 7-5. At

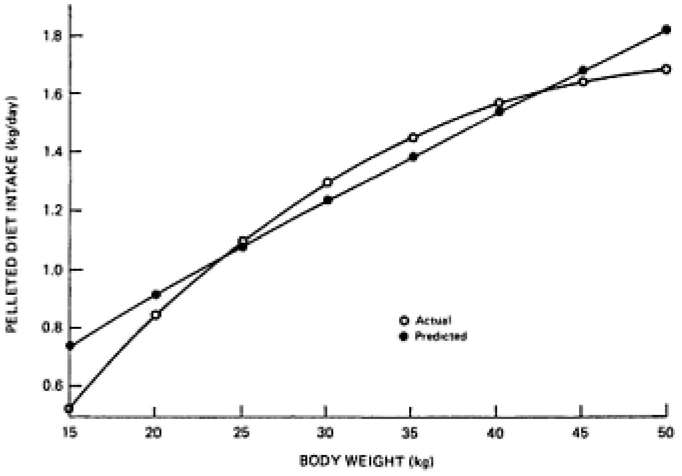

Figure 7-3
Pelleted diet intake of growing lambs.

most energy densities the legumes equation was within 5 to 10 percent of actual intake. Thus across both the ewe and wether evaluations, the legumes equation 4 appeared to be more consistently related to actual intake.

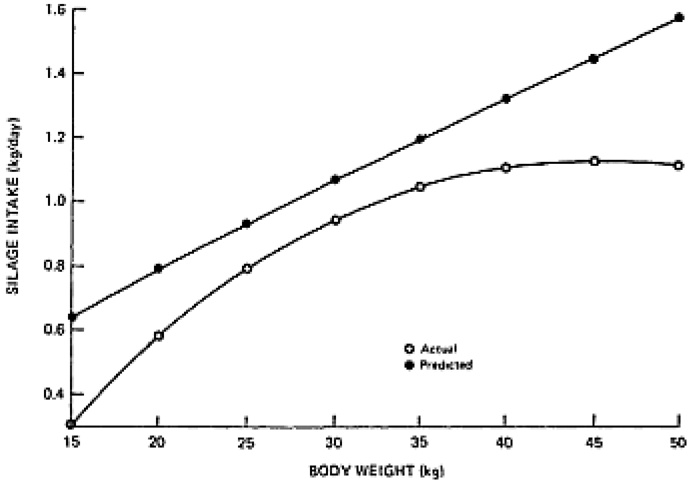

Figure 7-4
Silage intake of growing lambs.

MANAGEMENT TO MAXIMIZE INTAKE IN SHEEP

The physiological control mechanisms reviewed earlier that influence intake in sheep, and the prediction equations and adjustment factors that have been presented, suggest a number of management practices that influence intake as follows.

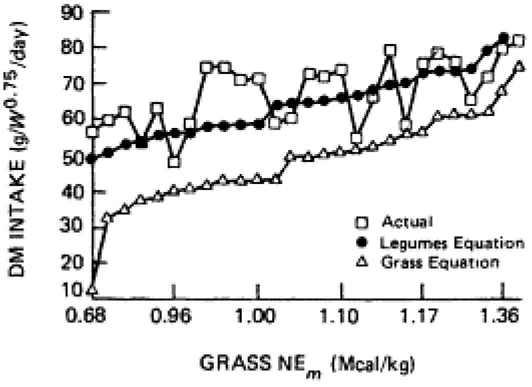

Figure 7-5
Dry matter intake of chopped grass by wethers. Actual data are those of Vona et al. (1984); data include 16 hays (cultivars of switchgrass, big bluestem, and tall fescue) collected in five states (Iowa, Kentucky, New Jersey, New York, and Pennsylvania) at three stages of growth (vegetative, early head, and early bloom).

1. For diets with high grain content, manage feeding to avoid a rapid drop in rumen pH and the rapid lactic acid buildup that follows because of the rapid proliferation of *Streptococcus bovis* at low pH. This is accomplished by:
   a. Maintaining a uniform, constant intake.
   b. Gradually moving to a full feed of grain by starting at 50 to 60 percent grain and then not increasing the grain level by more than 5 percent per day.
   c. Using a minimum coarse roughage level of 8 to 10 percent.
2. To maximize the use of high roughage diets, do the following:
   a. Avoid rapid filling. The stretch receptors will give a negative feedback, causing the animal to go off feed. Sheep appear to be more sensitive in this regard than are cattle.
   b. Consider processing to increase the rate of passage, especially in sheep. Digestibility will be reduced 5 to 10 percent, but the benefit of greater energy intake to more nearly meet maintenance needs or intake over maintenance that is available for productive functions may offset this effect. In many circumstances, the reduced wastage plus the greater rate of passage benefits may more than offset digestibility reduction and economic costs. Pelleting and fine milling of roughages will clearly be more beneficial in sheep than in cattle.

3. Balance dietary protein so that both rumen and animal needs are met. Diet formulation systems under development will take this into account in a dynamic way. An inadequate supply of ammonia and some amino acids will limit ruminal microbial growth, reducing the rate and extent of digestion and thus the rate of passage. Metabolizable protein must also be balanced relative to metabolizable energy intake and the animal's potential for tissue or milk production.
4. When feeding high-forage diets to growing sheep, intake can be improved by feeding some grain continuously (ARC, 1980). The primary effect apparently is to increase the rate of passage of the total diet, avoiding the effect of the sensitive stretch receptors that sheep have. Although there will be some loss in digestibility of the forage due to associative effects, the benefits in intake in sheep, especially growing sheep, may be much greater than the loss due to associative effects.
5. Blending off-flavored feedstuffs into a total mixed ration will overcome the olfactory appetite control mechanism. Many by-products or waste feeds can be utilized when restricted to a limited percentage of the diet, which varies with the particular feed. A good guideline if that level is not known is to start at 10 percent of the diet DM, increase the level slowly until intake begins to be reduced, then stop just short of that point.
6. Protecting sheep from direct exposure to weather effects (storms and mud, for example) will allow intake to increase during cold weather and thus reduce their critical temperature. Protecting sheep from direct exposure to heat stress will prevent intake reduction, allowing energy intake over maintenance and, thus, performance to be maintained.
7. Identifying sheep selected for relative growth rate potential will likely improve intake due to a greater nutrient demand. Both sheep and cattle industries need to improve methods of identifying animals with this ability and methods of maintaining identity so that production of this type can be recognized and encouraged.

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