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Intestinal electrolyte distribution and Ca45 and Sr89 insorption in calves

Samuel Cassius Perry

To the Graduate Council:

I am submitting herewith a dissertation written by Samuel Cassius Perry entitled "Intestinal electrolyte distribution and Ca45 and Sr89 insorption in calves." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Animal Science.

R.G. Cragle, Major Professor

We have read this dissertation and recommend its acceptance:

R.H. Feinberg, J.T. Miles, R.L. Murphree, E.W. Swanson

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Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

March 8, 1967

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Major Professor

We have read this dissertation
and recommend its acceptance:

Eric W. Swanson

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INTESTINAL ELECTROLYTE DISTRIBUTION AND Ca^{45} AND Sr^{89} INSORPTION IN CALVES

A Dissertation

Presented to

the Graduate Council of

The University of Tennessee

In Partial Fulfillment

of the Requirements for the Degree

Doctor of Philosophy

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by

Samuel Cassius Perry

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CHAPTER I

INTRODUCTION

The translocation of substances from the lumen of the intestine into the blood or into extracellular space (absorption) is a complex phenomenon. Any process such as active transport, carrier-facilitated diffusion, diffusion across lipid layers or through pores, vesiculation or pinocytosis can be assumed to be involved in this translocation. The involvement of one or more processes in the absorption of a particular constituent often produces experimental results that are difficult to interpret. All of the factors involved in absorption will not be resolved until the structure of biological membranes is better understood. Knowledge of membrance structure is essential before the biologist can relate, with validity and reliability, structure to function, that is, intestinal epithelial cells to their function of absorption. Structural-functional relationships of membrances precedes an understanding of the organism's ability to exert physiologic control over a particular function. Obviously, the main function of the cell membrance is to maintain an organized intracellular environment consistent with its genetic direction. Studies concerned with the transfer of metabolites across cell membranes are of secondary importance only to the biosynthesis of the membranes themselves.

One of the most prominent environmental situations presented to the intestinal epithelial cell is the ionic composition in the ingesta.

Since the ingesta does not possess the ionic constancy of body fluids, variability in absorption of a particular metabolite is not only often encountered but probably should be expected. The effects of ionic environment have been investigated particularly in connection with the absorption of sugars.

Basically, this study represents a modest attempt to define the effects of some physical conditions in the intestinal lumen and their effects on the passage of certain cations in vivo. The objectives of this study were: (1) to determine the concentration of some inorganic constituents in the gastrointestinal tract of calves, (2) to compare the insorption of calcium, strontium, sodium, and potassium from jejunal and ileal segments of calves, (3) to determine the effects of ionic calcium and strontium alternation on subsequent insorption of these cations to the blood, (4) to determine the effects of hypertonic conditions in the lumen on the insorption of some major cations, and (5) to determine the effects of iodoacetate on the relative passage of calcium and strontium.

CHAPTER II

LITERATURE REVIEW

All of the factors involved in the absorption of cations from the gut will not be reviewed in this chapter. The author is cognizant that cation movement cannot be separated from the movement of anions and probably water. This review will be concerned with those aspects of cation absorption as related to the foregoing experiments. Excellent reviews of mineral metabolism are available which cover the intimate details of absorption of the major cations (Nicolaysen et al., 1953; Nicolaysen and Eeg-Larsen, 1953; and Comar and Bronner, 1964). Historical developments in a particular area will be reviewed only if they are pertinent to the dissertation but otherwise general statements will suffice. It is recognized that the physiological phenomenon of absorption per se cannot be divorced from its physiologic control within the animal. This important aspect will be covered when deemed pertinent for understanding some aspect of major significance in the dissertation.

I. SODIUM AND POTASSIUM ABSORPTION

The emphasis on sodium and potassium in ion transport studies has arisen from certain characteristic qualities of these elements: (1) their predominant concentration in extracellular and intracellular fluids and (2) that the movement of sodium and potassium ions is linked to the utilization of metabolic energy for maintenance of cellular ionic

composition and elaboration of secreted fluids. Perhaps the most impressive evidence of the nature of the latter is specificity of the cation requirements of sodium and potassium-stimulated adenosine-triphosphate-splitting enzyme system first described by Skou (1957).

The rumen has been reported capable of absorbing a large number of inorganic and organic substances. The barrier to absorption is a stratified squamous epithelium which, among those tissues used to study transport, perhaps most closely resembles frog skin. However, an important difference between these two epithelial surfaces is the absence of any demonstrable glands in the rumen (Barcroft et al., 1944; and Dobson et al., 1956). Dobson (1959) and Sperber and Hyden (1952) showed that sodium was transported from the rumen contents of anesthetized sheep to the blood against both a concentration and potential gradient. Studies by Parthasarathy and Phillipson (1953) did not demonstrate such ruminal sodium transport. The above discrepancy was partially resolved by transepithelial electrical potential, short-circuit current, and resistance measurements on isolated rumen epithelium (Stevens, 1964). Calculation of the partial sodium conductances indicated that the entire sodium flux could not be explained by active transport of sodium in the direction of rumen to blood. Stevens (1964) suggested that a portion of the sodium was transported by exchange diffusion or a sodium chloride transport system.

Knowledge concerning potassium transport across rumen epithelium is extremely limited. Sperber and Hyden (1952) found that potassium accumulated in a potassium-free solution, placed in a rumen pouch of the

goat, to a concentration of 27 mM./liter. Substitution of a portion of the sodium in rumen contents by potassium increased the electrical potential between blood and rumen contents in conscious sheep (Sellers and Dobson, 1960). These findings suggest that the rumen is relatively permeable to potassium and that the distribution of this ion might be explained by passive diffusion.

The intriguing nature of the omasum as a physiological structure has stimulated little research. Most of the research concerning this organ has been an assessment of its role in the rate of passage of ingesta (Phillipson and Ash, 1964). Very little research has been directed to ion transport studies. While it is known that the omasum is premeable to a number of ions its absolute absorptive function remains obscure.

The sodium and potassium fluxes from the abomasal contents to the blood and vice versa have not been adequately studied in the ruminant animal. With caution, it may be possible to extrapolate some of the results obtained from the non-ruminant animal to the ruminant animal. While certain characteristics may be peculiar to the species the basic processes involved in absorption may be very similar.

The movement or transfer of water and other substances from the intestinal contents to the blood has been defined as "insorption" and their reverse movement as "exsorption" (Hindle and Code, 1962). Absorption, or net gain to the body, results when the rate of insorption of a substance exceeds its rate of exsorption. When the reverse is the case and the gain has been to the intestinal contents, "enterosorption"

has occurred. Cope et al. (1943) demonstrated in dogs that radiosodium is much more slowly insorbed from secreting than from nonsecreting gastric pouches and that it is more quickly absorbed from the antral portion of the stomach where acid is produced. These observations have been confirmed in humans (Reitemeier et al., 1957) and in rats (Moll and Code, 1962). The above findings demonstrate that the dog's stomach, like that of man and the rat, offers a barrier to insorption of sodium which is more pronounced when acid is being secreted. This barrier has been defined further in dogs by the observation that cessation of sodium passage from gastric contents to blood is dependent on the presence of hydrochloric acid, whether from intrinsic or extrinsic sources (Code et al., 1956). Insorption of potassium was slower than the insorption of sodium and was independent of the presence of hydrochloric acid in the stomach of the dog (Moll et al., 1956) and the rat (Moll and Code, 1962).

Investigations have indicated a difference between absorption in the upper and lower portions of the small intestine (Visscher et al., 1944; and Bucher et al., 1950). The duodenum has been studied infrequently, and its function has seldom been contrasted with that of the more distal segments. Results of Code et al. (1960) with dogs indicated that the mucosa of the duodenum equilibrates its contents with blood by maintaining nearly equal and large movements of water and sodium in both directions, while that of the ileum is fixed to serve absorption of water and sodium. Sodium was always exsorbed into the duodenal contents in large quantities while little appeared in the ileal

contents (Hindle and Code, 1962). The exsorption of large quantities of sodium may aid the absorption of some substances in the distal portion of the small intestine. Curran (1960) has shown that absorption of water in rat ileum does not occur in the absence of solute movement. Hence, sodium added to contents in the duodenum may facilitate the absorption of water in the small intestine. The presence of sodium has been shown by others to be essential for insorption of glucose and some amino acids from the small intestine (Riklis and Quastel, 1958; and Csaky and Zollicoffer, 1960). The addition of large quantities of sodium to the duodenal contents may aid the absorption of these substances in the distal portions of the small intestine.

The rates of insorption and exsorption of potassium do not differ in the duodenum or ileum of the dog (Code et al., 1960), nor did these rates differ in the duodenum from those in the ileum. In individual control studies the concentration of potassium increased in ileal contents which may have been a consequence of net water absorption.

McHardy and Parsons (1957) found that the net movement of sodium from the jejunum of dogs was decreased with increasing hydrogen ion concentration. Acidification of duodenal and ileal contents decreased but did not stop the insorption of sodium in the canine small intestine (Code et al., 1960). The construction of the small intestine membranes apparently is such that, while hydrogen ions may compete for mechanisms of exit with sodium ions, a decisive advantage is not given to hydrogen ions, as is the case in the gastric mucosa.

The rate of insorption of sodium was much greater than the rate of potassium insorption from the jejunum of rats *in vivo* (Moll and Code, 1962). The differences in insorptive rates were not the consequences of changes in motor activity of the gut but represented a difference in the processes involved in their transfer across the mucosa. Curran and Solomon (1957) concluded from *in vivo* experiments that sodium is actively transported across the small intestine of rats. This finding was confirmed *in vitro* with everted jejunal and ileal segments from rats (Clarkson and Rothstein, 1960). Their study showed that sodium was transported against an electrochemical gradient by a highly specific mechanism while potassium always moved in the direction of the electrochemical gradient and much more slowly than sodium.

Code *et al.* (1960) reported that in the ileum of the dog the concentration of sodium decreased and that of potassium increased in a manner that maintained a constant total concentration of sodium plus potassium. In this respect the terminal portion of the ileum may respond similar to that of colonic pouches in dogs (D'Agostion *et al.*, 1953; and Cooperstein and Brockman, 1959). In their tests the concentration of sodium decreased and that of potassium increased in a reciprocal fashion during the first 3-6 hours of residence of an isotonic solution in a pouch of the colon. Work with chronic Thiry fistulas in dogs indicated that the concentration of both sodium and potassium increased in the ileum and sodium decreased while potassium increased in the large intestine (Berger *et al.*, 1959). It is likely that some other factor was present with the Thiry fistulas that was

absent in the other tests. It is known that Thiry-Vella fistulas atrophy with time. Most investigators (Budolfsen, 1955; and Fisher, 1955) have observed a net absorption of sodium from the ileum. Abnormal circumstances have produced an enterosorption of sodium and water to the contents of the ileum. Enterosorption of sodium to the ileum has been found in irradiated rats (Goodner et al., 1955) and when acid in high concentration is placed in the ileum of dogs (Code et al., 1960).

Insorption and exsorption of potassium has been measured across tubular segments of guinea pig ileum (Chujyo and Holland, 1962). The insorption of potassium was three times the exsorption in this in vitro preparation. Hurwitz (1960) showed in vitro with guinea pig ileum that the insorption and exsorption of potassium was proportional to the total quantities of exchangeable ion present in the tissue and in the surrounding medium.

II. CALCIUM ABSORPTION

The rumen appears to be unimportant as an organ of calcium absorption. Storry (1961b) calculated that the concentration of ultrafilterable calcium and magnesium in rumen fluid was insufficient for these elements to be absorbed as freely diffusing ions. Calcium and magnesium introduced into the isolated rumen behave differently than sodium, potassium, and chloride. Phillipson and Storry (1965) could not demonstrate loss of calcium and magnesium from the rumen even with solutions that were sufficient to overcome potential and concentration gradients. Their results did not support the contention that increased

potential differences between blood and rumen contents impede the uptake of calcium and magnesium from this organ (Annison and Lewis, 1959).

Knowledge concerning absorption of calcium and other cations from the abomasum and small intestines of the ruminant animal is in a fragmentary state. Storry (1961c) noted that practically all the calcium and magnesium in the abomasal contents was ultrafilterable primarily because of the hydrogen ion concentration in this region. The contents of the duodenum of sheep are acid also and neutrality is not reached until the contents are in the jejunum (Magee, 1961; and Hogan and Phillipson, 1960). Consequently the opportunities for absorption seem to be greatest in the abomasum and duodenum. However, a net loss of calcium could not be demonstrated from duodenal loops of sheep (Phillipson and Storry, 1965). Any insorption that occurred from this site was less than the quantity of calcium being exsorbed into the intestine. Storry (1961c) reported that decreasing the hydrogen ion concentration of abomasal contents in vitro reduced the concentration of ultrafilterable calcium and magnesium due to binding of these ions to suspended material in the ingesta. The bound and ultrafilterable forms of both elements were in equilibrium. The above study gives little credence to precipitation of calcium as calcium phosphate or magnesium as magnesium ammonium phosphate (Simensen, 1959). Calcium and magnesium soap formation was also eliminated as a major factor contributing to the reduced concentrations of ultrafilterable calcium and magnesium.

Studies concerning the mechanisms of calcium transport have been restricted to the smaller laboratory animals, namely, the guinea pig

and the rat. Schachter and Rosen (1959) first demonstrated that everted small intestinal sacs of the rabbit, rat, and guinea pig could transfer calcium against a concentration gradient. Such transfer of calcium was dependent on oxidative phosphorylation and on dietary vitamin D. The maximal rate of calcium transport in the rat occurred in everted sacs from the proximal small intestine (Schachter et al., 1960a). The active transfer was relatively specific for calcium and no significant accumulation of other alkaline earth cations related to calcium occurred in the serosal fluid. It was also demonstrated that the active transport of calcium in vitro was greater with gut-sacs from growing than from older rats and it was also greater with gut-sacs from pregnant than from non-pregnant rats. These findings possessed some similarities with the absorption of calcium in vivo. Nicolaysen (1951) observed that loops of the proximal small intestine in vivo rats absorbed calcium more rapidly than did loops from the distal portion. The effects of growth and age on the intestinal absorption of calcium in vivo (Hansard and Crowder, 1957) are similar to those obtained in vitro. Schachter et al. (1960a, 1960b) observations in vitro and corollary results in vivo led them to postulate that the active transport mechanism could increase the intestinal absorption of calcium facultatively to meet the requirements of the organism. Maintenance of rats on a low calcium diet and ultraviolet irradiation of intact rats increased the active transfer of calcium by everted gut sacs (Dowble et al., 1960). Similar results were obtained with respiring slices of the proximal small intestine from rats in vitro (Schachter et al., 1960b). In later work, Kimberg et al. (1961)

found that everted small intestinal gut sacs responded facultatively to a diet low in calcium by increasing the active transport of the cation. Also, vitamin D was required for the adaptive response of active transport in the duodenum and ileum. Schachter et al. (1961) showed that vitamin D was required for the active transport of calcium in vitro. The transfer of calcium against a concentration gradient with everted gut sacs from the duodenum of rats has been observed by other investigators (Wasserman, 1960; and Williams et al., 1961).

The importance of active transport for calcium absorption in vivo is not clear. Active transport of calcium has been demonstrated in vitro against calcium concentrations equal to that of normal plasma (Schachter and Rosen, 1959; and Williams et al., 1961). Therefore, active transport of calcium in vivo is at least possible. However, in the normal intact animal where the calcium concentration of the intestinal contents is generally greater than that of plasma, absorption could occur by diffusion mechanisms. This led Schachter and his colleagues (1959, 1960a) to suggest that active transport of calcium occurred in the duodenum and passive diffusion in the jejunum and ileum. Such a situation appears untenable in the normal animal since it has been demonstrated that only a small portion of the calcium absorption occurs in the duodenum (Cramer and Copp, 1959; and Harrison and Harrison, 1960). It is difficult to visualize that active transfer of calcium only in the duodenum would permit the animal to express physiologic control over calcium absorption due to the short effective absorption time in this region. Active transport of calcium may become an important mechanism

in vivo when dietary calcium is limited and an adequate gradient for calcium absorption by diffusion may not exist.

Harrison and Harrison (1960) measured the transfer of calcium across everted intestinal sacs from rats under slightly different conditions than those used by Schachter and Rosen (1959). The conditions were developed so that the rate of diffusion of calcium across the intestinal wall as well as active transport against a concentration gradient could be determined. Their results confirmed those of Schachter *et al.* (1959, 1960a) that active transport of calcium was localized in the proximal small intestine and was dependent on oxidative metabolism. However, vitamin D treatment increased the rate of diffusion of calcium along the entire length of the small intestine and was not inhibited by cyanide or anaerobic conditions. The vitamin D effect on calcium transfer was not a nonspecific alteration of the permeability of the intestinal wall to cations since no effect of vitamin D on sodium transfer was observed. In later work with everted gut sacs (Harrison and Harrison, 1965) observed that the intact intestinal mucosa presented a diffusion barrier to calcium and that this diffusion barrier was lessened by vitamin D treatment of the animal from which the intestine was obtained. The effect of vitamin D could be obtained only by administration of the vitamin to the animal some hours before the intestinal preparation was made. The apparent time lag between the administration of vitamin D and the enhancement of calcium absorption across the intestinal mucosa has been observed by other investigators (Lindquist, 1952; Carlsson and Hollunger, 1954). It has been variously

reported that little vitamin D-enhanced calcium absorption occurs until after 3-5 hours (Dowdle et al., 1960), 4-15 hours (Sallis and Holdsworth, 1962), or until 2-3 days (Schachter et al., 1961).

The latent period is apparently not due to the metabolic conversion of vitamin D to an active compound. Norman et al. (1964) found no metabolites of vitamin D_3-H^3 in the rat kidney or intestine which had full biological activity in comparison to the parent vitamin D_3-H^3.

It is not known whether the delay is due to slow absorption and transportation of the vitamin to active sites or whether the delay in biological response reflects some undefined induction process. The ability of actinomycin D to inhibit the action of a subsequent dose of vitamin D in promoting calcium absorption from the intestine is well documented (Norman, 1965; Zull et al., 1965; and Schachter and Kowarski, 1965). These findings lend credence to the concept that vitamin D may act by inducing the synthesis of the appropriate enzyme systems or the alteration of membrane structure necessary for calcium absorption. Recently, Wasserman and Taylor (1966) reported the formation or elaboration of a calcium-binding factor after administration of vitamin D_3 to rachitic chicks. The evidence suggests that the factor is a protein. Vitamin D_3-enhanced duodenal absorption of Ca^{47} in rachitic chicks occurred almost simultaneously with the appearance of the vitamin D_3-induced factor.

Schachter (1963) has summarized the studies from his laboratory which indicate that the transport of calcium across the intestinal wall involves two processes: (1) penetration of the diffusion barrier of the

mucosal epithelium and (2) the transport of calcium across the mucosal cell by an energy-dependent system which is most active in the duodenal portion of the small intestine. Harrison and Harrison (1960, 1965) proposed that vitamin D influences the first step by reducing the diffusion barrier to calcium. Schachter et al. (1959, 1960) found that vitamin D increased the maximum concentration difference which could be developed by the intestine under conditions in which the active transport of calcium against a concentration gradient was measured. The question arises whether these phenomena can be explained by a single effect of vitamin D on diffusibility of calcium or whether an action upon an active transport system is also involved. Harrison and Harrison (1960, 1965) suggested that although an effect both on diffusion which is independent of oxidative metabolism, and upon an energy-dependent active transport system may be demonstrated, it is possible that both may represent manifestations of a single process. This is explained by considering both steps involved in calcium transport as proposed by Schachter (1963). It has been suggested (Harrison and Harrison, 1960, 1965) that if the rate-limiting reaction in the active transport of calcium by the intestinal epithelial cell is the penetration of calcium across the luminal surface of the cell the increased permeability of this surface to calcium could result in an increase in the total transport. The maximum concentration difference developed by active secretion of calcium in the direction away from the intestinal lumen could vary with the concentration of calcium within the mucosal cell which would be limited by the rate of entrance of calcium across the

luminal surface. Recently, Schachter et al. (1966) have proposed that the first step in calcium absorption involves facilitated diffusion and the second process is active transport. It was also proposed that depending on conditions both processes can be rate-limiting.

Nicolaysen (1937) placed solutions containing different concentrations of calcium in ligated jejunal gut loops of rats in vivo and reported a greater absorption rate with added amounts of calcium. Similar results have been obtained by perfusing calcium solutions through healed Thiry-Vella fistulas in dogs (Robinson et al., 1941; and Cramer and Dueck, 1962). At low concentrations of calcium in the perfusate the rate of calcium absorption was proportional to the calcium concentration but at higher concentrations the rate decreased continuously (Cramer and Dueck, 1962). Cramer and Dueck (1962) also found that when 4 mM./l. of magnesium was added to the perfusing solution containing 12.5 mM. calcium per liter the maximum absorptive capacity (MAC) for calcium was decreased. The MAC for calcium in a calcium lactate (12.5 mM. Ca/l.) perfusate was 18.5 mg. calcium per hour. The MAC for calcium was reduced to 9.3 mg. calcium per hour upon addition of 4 mM. of magnesium per liter to the perfusate. This suggested that both may be carried by the same transport system. Magnesium competition with calcium absorption has also been observed in vitro (Schachter et al., 1960; and Hendrix et al., 1963). Cramer and Dueck (1962) interpreted the observations of the approach to a maximal absorption rate with increasing calcium concentration, the magnesium competition, and the conformity of the calcium absorption data to Michaelis-Menten kinetics

that calcium was absorbed by a carrier system which involved either active or facilitated transport. Cramer (1963) summarized his work suggesting that calcium absorption occurs by facilitated diffusion which may be modified to meet the needs of the body.

III. STRONTIUM ABSORPTION

Strontium absorption has usually been studied in comparison to calcium absorption. It has been shown repeatedly that the intestinal epithelium has the ability to differentiate between alkaline earth metal ions such that the efficiency of absorption for calcium > strontium > barium (Comar and Wasserman, 1964; and Lengemann, 1963). Although the precise factors which determine the differential transfer are unknown, such discrimination has been known to vary with the age of the animal and level of calcium in the diet (Comar and Wasserman, 1964; and Thompson, 1963). Comar et al. (1956) proposed the term "the strontium-calcium observed ration (OR)" to represent the differential metabolism of calcium and strontium. The OR represents the over-all discrimination between two compartments and was defined as:

$$\text{OR sample/precursor} = \frac{\text{Sr/Ca in sample}}{\text{Sr/Ca in precursor}} .$$

The addition of stable calcium and strontium to the diet has not proven to be an effective means of reducing the deposition of radio-strontium in the skeleton of the chick (Mraz, 1961) and rat (Hegsted and Bresnagan, 1963). These studies demonstrated that the intestinal concentration of radiostrontium was not effectively diluted by addition of

either calcium or strontium to the diet. Such a phenomenon has also been observed in dairy cows and goats (Wasserman et al., 1960). This effect is inconsistent inasmuch as elevated dietary calcium has been shown to decrease the ultimate body burden of radiostrontium in rats (Wasserman and Comar, 1960; and Palmer et al., 1958). It has also been observed in rats that increased dietary calcium decreased the absorption of Ca^{45} and Sr^{85} effectively and to about an equal degree, whereas a four-fold increase in strontium intake did not reduce the absorption and retention of Sr^{85} (Wasserman et al., 1957). However, dietary strontium reduced the skeletal retention of radiostrontium three- to four-fold in young pigs (Bartley and Reber, 1961).

That the intestinal membrane discriminates against strontium in favor of calcium has been shown by a number of investigators (Comar et al., 1957; Cragle and Demott, 1959; and Hegested and Bresnagan, 1963). Cragle and Demott (1959) reported that radiocalcium was absorbed 2.9 times more readily than radiostrontium by dairy cows. Strontium discrimination has also been demonstrated in the rat by the technic of in vivo intestinal perfusion. Palmer and Thompson (1961) reported that the percentage of strontium absorbed ranged from 0.3 to 0.6 that of calcium. There was no evidence of discrimination in the reverse movement of calcium and strontium from blood to intestine. The discrimination that occurs in the absorption process appears to be a dominant factor in determining over-all strontium-calcium relationships.

The progress and rate of absorption of radiostrontium through the intestinal tract of rats has been studied in vivo (Cramer and Copp, 1959).

The highest initial rate of absorption occurred in the duodenum with jejunum, ileum, colon, and stomach following in decreasing order. However, due to the rapid passage of radiostrontium through the duodenum and jejunum, the largest actual effective absorption occurred in the ileum (65 per cent), with smaller contributions by the jejunum (17 per cent), colon (8 per cent), duodenum (7 per cent), and stomach (2 per cent).

Wasserman (1960) did not find strontium transported against a concentration gradient in everted gut sacs from rats. It was demonstrated that strontium-calcium discrimination under given conditions was dependent upon a metabolically active membrane. However, Kimberg et al. (1961) reported that strontium was transferred against a concentration gradient in duodenal sacs of rats on a calcium deficient diet. No differences were found in calcium and strontium transport between duodenal and ileal segments in situ of parathyroidectomized rats compared to normal controls (Wasserman and Comar, 1961).

It has become increasingly apparent that there exists an interrelationship between calcium, magnesium, and strontium for transport in both the intestine and the renal tubule. Berglund and Forster (1957) indicated that there may be competition between calcium and magnesium for transport by the renal tubule of an aglomerular teleost. Recently, it has been postulated that calcium and magnesium compete for transport both in the intestine and in the renal tubule of rats (Alcock and MacIntyre, 1960, 1962). The competitive relationship between calcium, magnesium, and strontium for transfer across everted gut sacs from

calcium and magnesium deprived rats has been studied (Hendrix et al., 1963). It was found that calcium ions reduced the rate at which Sr^{85} crossed the duodenal wall. This was interpreted to be consequence of a competitive relationship between calcium and strontium ions for active transport. Strontium ions were less effective than calcium ions in reducing the rate of transport of Sr^{85} by the duodenum. The active uptake of Ca^{45} by the duodenum and ileum was inhibited by strontium and magnesium ions. Hendrix et al. (1963) concluded that, at least in part, calcium, strontium, and magnesium absorption occurs by a common pathway in the gut. However, observed differences in the competitive effect in different portions of the intestinal tract suggested that the absorption of a particular cation may also involve other pathways. Peters and Walser (1966) studied cation transport across everted rabbit gall bladders. Their results showed that cations having a larger or smaller crystal radius than sodium were transported less readily. A significant observation was that the gall bladder could be induced to transport as great of quantities of any one of the cations studied as of sodium and in many instances at comparable rates. Peters and Walser (1966) postulated the existence of a common cation pump for transport in the rabbit gall bladder. They suggested that "the prevalent view that biological effects of individual ions are highly specific may require some revision; a spectrum of ionic effects in relation to some parameter of ion size and charge may serve better to describe a number of biological processes."

CHAPTER III

MATERIALS AND METHODS

I. UNABSORBED MARKER EXPERIMENT

The primary objective of this study was to determine the effects of extremely different rations upon the concentration of some inorganic constituents in intestinal contents of calves. To study these effects 11 Holstein calves, similar in age and body weight (mean = 150 kg.), were divided into three groups. Group A (four calves) was fed a semi-purified ration similar to one used successfully for lambs (Table I, Matrone et al., 1959). Group B (four calves) was fed a concentrate ration that consisted of 77.5 per cent ground ear corn, 5.0 per cent alfalfa meal, 12.0 per cent cottonseed meal, 5.0 per cent molasses, and 0.5 per cent each of bone meal, dicalcium phosphate, and trace mineralized salt. Group C (three calves) was fed a ration that consisted of the above concentrate mixture and alfalfa hay. Twice daily all the calves were fed constant amounts of their respective feed. Water was offered ad libitum and no measurement was made of daily consumption. The amount of feed that was offered at each feeding was initially determined by the amount they would consume within 1 hour during the adjustment period. The daily intake of each calf was constant for 8 days prior to sacrifice. Immediately before each feeding Groups A and C received 25 μCi. of Ce^{144} as an unabsorbed marker in a gelatin capsule.

TABLE I

COMPOSITION OF SEMIPURIFIED RATION

Component	Per cent
Casein	26.5
Glucose	31.8
Corn strach	17.7
Hydrogenated vegetable oil	3.5
$KHCO_3$	4.4
$NaHCO_3$	7.3
Vitamin mixture[a]	4.4
Mineral mixture[b]	4.4

[a]Vitamin mixture (5 lb.): thiamine HCl, 400 mg.; riboflavin, 850 mg.; nicotinic acid, 1.13 gm.; Ca pantothenate, 1.42 gm.; pyridoxine HCl, 570 mg.; folic acid, 57 mg.; p-amino-benzonic acid, 1.13 gm.; inositol, 11.35 gm.; biotin, 11.4 mg.; choline chloride, 113.45 gm.; menadione, 115 mg.; 0.1 per cent B_{12} in mannitol, 4.66 gm.; alpha-tocopherol acetate, 570 mg.; glucose, 2,132 gm. 4,000 I.U. of vitamin A and 400 I.U. of vitamin D administered/day/45 kg. body wt. via capsules.

[b]Mineral mixture (5 lb.): $CaHPO_4$, 818 gm.; KCl, 273 gm.; NaCl, 239 gm.; $MgSO_4$, 204 gm.; $CuSO_4 \cdot 5H_2O$, 893 mg.; $FeSO_4 \cdot 2H_2O$, 7,648 gm.; $MnSO_4 \cdot H_2O$, 1,399 mg.; Zno, 2,263 mg.; $CoCO_3$, 9 mg.; KO, 6 mg.; glucose, 722 gm.

Each calf in Group B received 0.5 gm. of Cr_2O_3 per feeding as an unabsorbed marker. The Cr_2O_3 was mixed with 10 gm. of starch which was then mixed into the feed that was offered at each feeding. It has been established that Ce^{144} is comparable to Cr_2O_3 when used as an unabsorbed marker (Cragle et al., 1965).

The calves were confined in metabolism stalls for a preliminary adjustment period (3 weeks for Group A) and for administration of the unabsorbed markers. On the morning that the calves were sacrificed, the usual feeding procedure was followed with regard to the quantity of feed offered and either Ce^{144} or Cr_2O_3. All the calves were sacrificed approximately 4 hours after feeding. After sacrifice the gastro-intestinal tracts were tied off, removed, and divided into the reticulo-rumen, omasum, abomasum, six equal sections of the small intestine, cecum, and two sections of the large intestine. Contents of each section were weighed and mixed before sampling. Samples (2-4 gm.) of the ingesta from each segment were placed into plastic tubes for counting the Ce^{144} in a gamma spectrometer (Groups A and C). Chromic oxide in the ingesta was determined by the method of Brisson (1956).

Samples of the ingesta were weighed into crucibles and dried 24 hours at 100° C. After a dry weight was obtained the samples were ashed at 600° C. The ash was dissolved in 6 N. HCl and made up to a constant volume. Aliquots of the ashed samples were used for all mineral determinations.

Sodium and potassium concentrations in the ingesta were determined by the flame photometer (Model 21, Coleman). Calcium and magnesium were

determined by the complexometric titration method of Kamal (1960) for the first two groups (A and C) and by an atomic absorption spectrometer (Model 303, Perkin-Elmer) which became available for the last group (B). Nitrogen was determined by the Kjeldahl procedure according to A.O.A.C. (1955).

II. IN VIVO INTESTINAL SEGMENTS

Animals. A total of 32 calves were utilized for this phase of experimentation. These calves were represented by both sexes and a number of breeds and cross-breds. The calves used in these experiments ranged from 32-64 kg. body weight (mean = 52 kg.). All the calves received some milk (some were only milk-fed) and alfalfa hay ad libitum. The milk offered at each feeding was limited depending on the size of the calf. The calves ranged in age from 2-8 weeks with an average age of 5 weeks.

Experiments. A total of six experiments were conducted utilizing the in vivo isolated gut technique. Briefly, the objectives of these six experiments were: (1) To compare the insorption of Na^{24}, K^{42}, Ca^{45}, and Sr^{89} from isolated jejunal and ileal segments. Eight calves were utilized in this experiment. (2) To determine the effects of isomolar replacement of calcium by strontium in the luminal solutions upon the relative insorption of Ca^{45} and Sr^{89}. Three adjacent jejunal segments were isolated in each of four calves. The same jejunal solution from the above experiment was used with the foregoing alterations. The solutions injected into the lumen contained 5.0 mM. Ca/l., 2.5 mM.

Ca/l. and 2.5 mM. Sr/l., and 5.0 mM. Sr/l. (3) To determine the effects of hypertonic conditions in the gut lumen upon the insorption of Ca^{45} and Sr^{89}. Three adjacent jejunal segments were isolated in each of four calves. The solutions contained the same ionic composition as the jejunal solution in Experiment 1. The osmolality of the solutions was 288, 383, and 553 milliosmols (mOs.). (4) Experiments 2 and 3 were replicated in one experiment on the same isolated jejunal segments. The experimental design for this experiment is given in Table II. Two jejunal segments were isolated on each of eight calves. The respective solutions were the same as those previously mentioned. The treatments of 5.0 mM. Ca/l. and 2.5 mM. each of Ca and Sr/l. were altered on the same segment. Solutions containing 5.0 mM. Ca/l. with an osmolality of 296 and 396 mOs. were altered on another isolated segment of the same calves. (5) To compare the effects of varying concentrations of calcium or strontium in the solutions upon the subsequent insorption of Ca^{45} and Sr^{89}. Six calves were utilized to determine the insorption of Ca^{45} and Sr^{89} from solutions containing 1 mM. Sr/l., 5 mM. Sr/l., 1 mM. Ca/l., 5 mM. Ca/l., and 10 mM. Ca/l. Three or four adjacent jejunal preparations were made on each of the six calves. (6) To determine the effects of time after initiation of the isolated intestinal segments upon the relative insorption of Ca^{45} and Sr^{89}. Jejunal and ileal preparations were made on two calves to determine if the preparation possibly altered the physiological mechanism involved in insorption of Ca^{45} and Sr^{89}.

TABLE II

DESIGN FOR ALTERING TREATMENTS ON THE SAME ISOLATED JEJUNAL SEGMENTS

Calf	Segment	Treatment		
		1st	2nd	3rd
1	A	5.0 mM. Ca/l.	2.5 mM. Ca/l. and 2.5 mM. Sr/l.	Iodoacetate
	B	296 mOs.	396 mOs.	Iodoacetate
2	A	2.5 mM. Ca/l. and 2.5 mM. Sr/l.	5.0 mM. Ca/l.	Iodoacetate
	B	396 mOs.	296 mOs.	Iodoacetate
3	A	5.0 mM. Ca/l.	2.5 mM. Ca/l. and 2.5 mM. Sr/l.	Iodoacetate
	B	296 mOs.	396 mOs.	Iodoacetate
4	A	2.5 mM. Ca/l. and 2.5 mM. Sr/l.	5.0 mM. Ca/l.	Iodoacetate
	B	396 mOs.	296 mOs.	Iodoacetate

NOTE: The above design was replicated with four more calves.

Surgical preparation. The basic techniques involved in the surgical preparation will be described in this section. The modifications of the technique described peculiar to a particular experiment will be discussed in the next chapter.

The calves used for the in vivo insorption studies were removed from feed approximately 12 hours prior to the experiment. In the initial experiments the calves were anesthetized using electrical anesthesia and in later experiments with pentobarbital sodium (Diabutal, Diamond Laboratories, Inc., Des Moines, Iowa). The rate of administration of pentobarbital sodium was approximately 30 mg./kg. body weight and adjusted to effect. The anesthesia produced by pentobarbital sodium was superior to electrical anesthesia for these studies. Physiological saline (0.154 M.) was slowly "dripped" into the right jugular vein during the experimental period.

The calf was placed and secured on the operating table after the desired anesthetic effect was attained. An abdominal incision, approximately 25 cm., was made right of midventral but the peritoneum was left intact. A large plastic bag was then sutured to the musculature of the lower incised surface. An incision was then made in the peritoneum and a portion of the intestinal tract was taken from the abdominal cavity. The area of intestines desired for study (and portions of the tract in the immediate proximity) was placed in the plastic bag to prevent loss of heat and fluids. The intestinal portions under study were continuously bathed with warm (37° C.) physiological saline.

The mesenteric vessels in the calf are arranged in anastomosing loops from which tributaries arise to and from the gut. This is the basic architecture but some segments possessed more desirable conformation for experimentation, as with, the size of the vein in comparison to the length of the intestinal segment. The selection of the segment preceded the removal of its contents. This was accomplished either by the manual manipulation of the ingesta caudally or by cutting one end of the intestinal segment and flushing with warm (37° C.) physiological saline. Isolated segments were prepared by placing ligatures along the flushed section of the intestine. The length of the intestinal segment under study ranged from 25-60 cm. depending on the intestinal architecture and location along the gastrointestinal tract. The mesenteric vein which carried all the blood from the isolated segment was selected for cannulation, separated from its associate artery, and two nylon ligatures were placed around the vein but not drawn tightly. The two veins of the anastomosing loops were ligated to prevent blood from the isolated segment being drained by other mesenteric veins that were not cannulated. The position of ligation of the vein loops corresponded to the ligation of the intestinal segment. All veins which did not carry blood from the isolated segment, but which did join the mesenteric vein below the point selected for cannulation, were ligated to prevent blood from other intestinal areas from entering the vein selected for cannulation.

The calf was then given 10,000 U.S.P. units of heparin sodium (Abbott Laboratories) into the right jugular vein. The ligature on the

mesenteric vein distal to the intestine was tied tightly and a small incision was made in the vein between the tightened ligature and the remaining loose ligature. A cannula of polyethylene tubing (200 or 260 depending on the size of the vein) was placed into the vein through the incision and past the loose ligature. The ligature was tightened to hold the cannula in place and to prevent leakage of blood around the cannula. This preparation made it possible to collect all the blood and only the blood draining the isolated intestinal segment.

Usually, two or three preparations were made on each calf. In the experiments where three preparations were made these were adjacent to each other and blood collections were made simultaneously from each. A constant volume of blood was collected for each sample and its time recorded during the experimental period.

The calf was sacrificed at the conclusion of each experiment with an intravenous injection of saturated KCl. The intestinal tract was then removed and the exact location of the preparations was determined. The intestinal segment(s) were removed, measured, and taken for analyses.

Composition of gut solutions. The basic composition of the gut solutions is given in Table III. The values for the mineral concentrations of the jejunal and ileal regions were estimated from the unabsorbed marker experiment. The basic solution for all treatments was adjusted to pH 6.0 with HCl and had an osmolality of 295 mOs. The jejunal solution listed in Table III was the same for all experiments on the isolated adjacent jejunal segments. In the experiments where the

TABLE III

COMPOSITION OF GUT SOLUTIONS

Cation	Jejunal	Ileal
	mM./l.	
Ca	5.3 (2.5)(5.0)	16.8
Sr	(2.5)(5.0)	
Mg	8.8	15.0
P	16.3	15.1
Na	115.0	92.7
K	20.5	15.4

concentration of calcium and/or strontium was altered this was accomplished on an equimolar basis and the concentration of other cations remained unchanged. To determine the effects of hypertonicity upon the insorption of Ca^{45} and Sr^{89} the basic 5.0 mM. Ca/l. jejunal solution was used with the addition of polyethylene glycol (M.W. 4,000) to raise the osmolality of the solutions to 383 and 553 mOs. This required approximately 50 and 110 gm. of polyethylene glycol/l. respectively. The osmolality of the solution was determined by an osmometer (Advanced Instruments, Inc., Model 65-31) and expressed as mOs. The concentrations of all cations remained the same in these solutions with the exception of Na which was reduced as a consequence of the volume of polyethylene glycol added. In other experiments where a number of calcium and strontium concentrations were used this was done by a specific alteration of calcium or strontium while the concentrations of the other cations were unchanged. However, the concentrations of Na in the solutions were slightly changed because 0.9 per cent NaCl was used to bring all solutions to a constant volume. All solutions injected into the lumen contained approximately 75 μCi. each of Ca^{45} and Sr^{89} and 150 μCi. of Na^{24} or K^{42} (in some experiments).

Analytical procedures. The packed red cell volume was determined by the microhematocrit method. The blood plasma was separated from the red cells by centrifugation at 1,400 X g. for 15 minutes. Duplicate samples of blood plasma (1-15 ml.) were pipetted into crucibles and dried at 90° C. and subsequently ashed at 600° C. overnight. The ashed

samples were dissolved in 1 ml. of 6 N. HCl and diluted to 25 ml. Aliquots of these samples were taken for Ca^{45} and Sr^{89} analyses.

Ca^{45} and Sr^{89} were counted under a micro-mil window, continuous gas flow, automatic planchet changer, Geiger-Müller tube (Nuclear-Chicago). Standard samples prepared from dilutions of the dosing solutions were counted with the experimental samples. A comparison of the standard sample count with that of the experimental sample allowed the results to be expressed in terms of the per cent of the administered dose.

Radiocalcium and radiostrontium were precipitated as oxalates in a tared cup assembly (Comar et al., 1951). Stable calcium (4 mg.) was added to the ashed plasma aliquots to insure more complete precipitation of the radioisotopes. Ca^{45} and Sr^{89} were differentially counted using an aluminum absorber with a density greater than 55.2 mg./cm.^{2} to distinguish between the beta energies. No Ca^{45} emissions could be detected through the absorber. A Ca^{40}-Sr^{89} oxalate was used to calculate the per cent of Sr^{89} emissions that were absorbed. A self-absorption correction table prepared at this laboratory was used to correct for Ca^{45} self absorption.

Na^{24} and K^{42} were assayed in a gamma ray spectrometer (Nuclear-Chicago). The gamma emissions were determined over the photopeak and the contribution of counts by beta emitters was negligible (<1 per cent) in the blood samples that contained Na^{24} or K^{42}, Ca^{45} and Sr^{89}. In those experiments where Na^{24} or K^{42} was present, 3 ml. of blood were pipetted into tubes for radioassay. The decay of Na^{24} and K^{42} during

the counting of a number of samples was adjusted by counting repeated standards and by calculating the percentage decline in counts for a specified time interval after initiation of radioassay.

CHAPTER IV

RESULTS AND DISCUSSION

I. UNABSORBED MARKER EXPERIMENT

The concentrations of many minerals have been determined at various locations along the gastrointestinal tract of ruminants. The ultrafilterable concentration of Ca and Mg have been measured in gut contents of slaughtered cows (van Weerden, 1961) and anesthetized sheep (Storry, 1961). Van't Klooster (1964) determined the concentration of Na, K, Ca, and Mg in intestinal contents by a dialysis procedure using fistulated sheep.

The insorption and exsorption of minerals throughout the gastrointestinal tract does not permit the quantitative expression of absorption and/or enterosorption of a particular constituent. Therefore, a commonly used method for determining absorption or enterosorption has been to compare intestinal constituent concentrations to the concentration of an unabsorbed marker. The sites of absorption of Ca and P (Chandler and Cragle, 1962), I (Barua et al., 1964), and Zn (Miller and Cragle, 1965) have been determined in calves through the simultaneous administration of an unabsorbed marker with the feed and the respective isotope.

The average daily intakes of the respective rations were: A, semipurified--2.0 kg.; B, concentrate--2.8 kg.; C, concentrate and hay--2.1 kg. concentrate and 1.2 kg. hay. The total dry matter in the tract

at the time of sacrifice averaged 1.0, 3.5, and 5.3 kg. for Groups A, B, and C, respectively. The average percentages of the total dry matter in the tract that was present in the rumen were: semipurified, 70 per cent; concentrate, 65 per cent; and concentrate and hay, 58 per cent. These values reflect the differences in the total dry matter content in the tract as a result of differences in intake, rate of passage, and digestibility of the rations. The dry matter digestibility in the rumen of calves fed the semipurified ration was 60 per cent compared to 10 per cent for the calves fed the other two rations. Dry matter digestibility was calculated by marker ratio techniques. The values of dry matter digestibility in the rumen are only estimates since sampling procedures are of utmost importance to obtain a representative sample from the heterogenous ruminal contents. However, it is probable that the semipurified ration would be highly fermentable in the rumen and the quantity of ingesta entering and leaving the omasum would be less. The semipurified ration would promote fermentative digestion in the rumen at the expense of hydrolytic digestion in the intestine. No significant amount of ingesta was present in omasum of the calves fed the semipurified ration. Many aspects of the physiological mechanisms involved in the functioning of the omasum remain to be explored. Briggs (1961) reported that approximately 7 per cent of the volume entering the omasum could not be accounted for in the material leaving the organ. This value does not support the contention that approximately 50 per cent of the water entering the omasum is absorbed. However, Briggs (1961) used polyethylene glycol as an unabsorbed marker which is water soluble. In this

study by comparing the concentration of the unabsorbed marker in the ruminal contents to the concentration in the omasal contents a value of approximately 60 per cent of the water in the ruminal contents could not be accounted for in the omasal contents. This does not necessarily indicate that 60 per cent of the water entering the omasum is absorbed. It may indicate that the material entering the omasum is compacted and the soluble portion passed into the abomasum. This would be consistent with the visual observations of ingesta leaving the omasum (Phillipson and Ash, 1964). If this occurred to a great extent a water soluble marker would underestimate the actual water absorption if measured for a relatively short period of time. Conversely, if the unabsorbed marker traveled with or adsorbed onto the undigested portion of the ingesta, it would overestimate the actual absorption of water or other constituents by the omasum. A high percentage of Ce^{144} adsorbs onto the undigested residues (Miller et al., 1966).

The significantly lower ($P<.05$) dry matter content already present in the rumen of the calves fed the semipurified ration and the higher digestibility of the ration probably accounts for the lower dry matter content in the small intestine and cecum of this group compared to the other two groups (Table IV). There were no group differences in ingesta moisture content in the region of the distal large intestine.

The calcium concentration in the intestinal contents are given in Table V. All values in this and subsequent tables are expressed as milligrams/gram of feed that was ingested. These values are obtained by determining the quantity of the unabsorbed marker present in a gram of

TABLE IV

DRY MATTER CONCENTRATIONS IN INTESTINAL CONTENTS OF CALVES FED SEMIPURIFIED, CONCENTRATE, AND CONCENTRATE AND HAY RATIONS[a]

Section of G.I. tract	Semipurified	Concentrate	Concentrate and hay
	%	%	%
Rumen	6.9 ± 1.1	18.5 ± 3.8	17.6 ± 0.9
Omasum[b]		30.9 ± 1.2	25.1 ± 1.5
Abomasum	10.8 ± 4.4	21.2 ± 2.9	13.5 ± 5.4
SI-1[c]	7.8 ± 1.1	11.0 ± 2.8	11.3 ± 2.8
SI-2	6.2 ± 1.7	9.7 ± 0.7	9.6 ± 0.3
SI-3	5.8 ± 1.1	8.7 ± 2.1	7.3 ± 0.8
SI-4	5.3 ± 0.4	8.1 ± 1.3	6.6 ± 0.7
SI-5	4.6 ± 1.9	8.0 ± 0.6	6.9 ± 1.2
SI-6	5.0 ± 2.0	11.2 ± 2.4	10.0 ± 0.5
Cecum	9.4 ± 2.7	17.5 ± 1.4	14.1 ± 1.1
LI-1[d]	14.4 ± 4.2	19.2 ± 0.1	15.0 ± 1.7
LI-2	21.9 ± 1.4	22.9 ± 1.4	18.7 ± 2.2

[a]Values expressed as mean ± S.D.

[b]No ingesta in omasum of calves fed the semipurified ration.

[c]SI = small intestine.

[d]LI = large intestine.

TABLE V

CONCENTRATION OF Ca IN INTESTINAL CONTENTS OF CALVES FED A SEMIPURIFIED, CONCENTRATE, OR CONCENTRATE AND HAY RATION[a]

Item	Semipurified	Concentrate	Concentrate and hay
	mg./gm. feed ingested		
Rumen	3.8 ± 0.7	4.4 ± 0.8	8.0 ± 3.0
Omasum[b]		3.0 ± 0.6	7.8 ± 1.0
Abomasum	3.6 ± 0.9	8.2 ± 2.3	10.4 ± 1.4
SI-1[c]	4.0 ± 0.7	3.9 ± 1.7	5.1 ± 1.5
SI-2	3.8 ± 1.3	2.9 ± 0.9	5.7 ± 1.5
SI-3	3.1 ± 0.6	2.8 ± 0.6	5.6 ± 1.0
Cecum	2.8 ± 0.8	2.1 ± 0.5	4.8 ± 1.4
LI-1[d]	2.5 ± 0.4	1.9 ± 0.6	4.5 ± 1.0
LI-2	2.7 ± 0.4	1.8 ± 0.3	4.5 ± 1.0
Ca in feed (mg./gm.)	5.1	6.7	7.5
Av. daily intake (gm.)	9.6	19.0	20.3

[a]Values expressed as mean ± S.D.

[b]No ingesta in omasum of calves fed the semipurified ration.

[c]SI = small intestine.

[d]LI = large intestine.

feed that was fed and comparing the same quantity of marker in the ingesta to the determined concentration. This can be expressed by the following equation:

$$\frac{\% \text{ marker/gm. feed}}{\% \text{ marker/gm. ingesta}} \times \text{mg. nutrient/gm. ingesta} = \text{mg. nutrient/gm. feed ingested.} \quad (1)$$

Enterosorption has occurred if these values are greater than the amount originally contained in the feed. Conversely, if the values are less than the amount in the feed, net absorption has occurred. The contents of small intestinal segments was combined and reduced to three for mineral analyses. The distribution of Ca in the intestinal contents compare favorably with the values reported by Chandler and Cragle (1962). However, it appears unlikely that Ca is absorbed from the rumen in the quantity that is indicated by the calves that received the semipurified amd cpmcemtrate rations. Storry (1961a) could not demonstrate a net loss of Ca or Mg ions from the rumen even with solutions that were sufficient to overcome potential and concentration gradients. The slight gain in the ruminal calcium concentration of the calves that received the concentrate and hay ration could be due to an influx of Ca into the rumen via the saliva (Storry, 1961a). No enterosorption or absorption of Ca occurred in the omasum. The abomasum presented somewhat different results. Enterosorption of Ca was evident in some calves while in others absorption apparently occurred. Yang and Thomas (1965) reported that in 14 of 24 calves more Ca was absorbed than enterosorbed in the abomasum. It is known that practically all of the Ca in the

abomasal contents is ultrafilterable because of the hydrogen ion concentration (Storry, 1961a, 1961b). Therefore, the best possible milieu exists in the abomasal contents for absorption of Ca but under certain conditions enterosorption is indicated. Phillipson and Storry (1965) could not demonstrate a net loss of Ca from the duodenum where the environment in the ingesta would be similar to that present in the abomasum.

The major region of Ca absorption was the small intestines in all the calves. Very little change occurred in the cecum and large intestine. The Ca concentration in the contents from the distal small intestines and large intestines that received the concentrate and hay ration was higher ($P<.05$) than the other two groups. A partial explanation for this may be that a larger portion of the calcium in the contents from these locations was in a complexed form. Since young calves are known to be very efficient in their ability to absorb Ca (Cragle et al., 1965), it would appear that the observed difference was not due to an alteration of intestinal permeability. It would be more likely that a larger portion of the Ca in these regions was absorbed onto the undigested residues (Storry, 1961b) thereby reducing the Ca concentration available for absorption.

The intestinal Mg concentrations are given in Table VI. No change occurred in the ruminal Mg concentration in relation to the feed that was ingested. While it is possible that the omasum may be premeable to Mg (Stewart and Moodie, 1956), it is unlikely that the absorption from this organ was as great as indicated in Group C.

TABLE VI

CONCENTRATION OF Mg IN INTESTINAL CONTENTS OF CALVES FED A SEMIPURIFIED, CONCENTRATE, OR CONCENTRATE AND HAY RATION[a]

Item	Semipurified	Concentrate	Concentrate and hay
	mg./gm. feed ingested		
Rumen	0.9 ± 0.4	2.7 ± 0.5	2.6 ± 0.1
Omasum[b]		1.7 ± 0.4	1.6 ± 0.1
Abomasum	0.9 ± 0.4	1.7 ± 0.8	2.9 ± 0.1
SI-1[c]	3.0 ± 1.9	4.5 ± 1.6	3.3 ± 0.8
SI-2	2.1 ± 1.5	3.1 ± 1.6	2.4 ± 0.3
SI-3	1.5 ± 0.6	2.9 ± 0.9	2.2 ± 0.5
Cecum	0.8 ± 0.4	2.1 ± 0.5	1.7 ± 0.1
LI-1[d]	0.8 ± 0.3	1.9 ± 0.4	1.6 ± 0.2
LI-2	0.6 ± 0.2	1.7 ± 0.1	1.7 ± 0.4
Mg in feed (mg./gm.)	0.9	2.5	2.6
Av. daily intake (gm.)	1.6	7.0	7.0

[a]Values expressed as mean ± S.D.

[b]No ingesta in omasum of calves fed the semipurified ration.

[c]SI = small intestine.

[d]LI = large intestine.

Enterosorption of Mg occurred in the proximal small intestine of all calves. Storry (1961a) found that bile and pancreatic secretions contained appreciable quantities of both calcium and magnesium. The quantity of calcium and magnesium entering the proximal small intestine is of such magnitude that absorption of these elements cannot be detected in passage through this region. Absorption occurred in passage through the small intestines with little change thereafter. This is in contrast to the results of Smith (1959a, 1959b) in which it was reported that the absorption of Mg in calves occurred principally in the large intestines. However, these data are in agreement with the results of Stewart and Moodie (1956) and Field (1961) that the major region of Mg absorption is the small intestines. The apparent absorption of Mg on all the rations was 35 per cent. Smith (1962) reported Mg absorption of 30-40 per cent in milk-fed calves. In later work, Smith (1966) found that in calves fitted with ileal reentrant fistulas that Mg had a quantitative effect upon the ileal water emergence suggesting that it was present in a soluble or ionic form. If the calves in this study behaved similarly, it would appear that other factors may be more important in Mg absorption than its presence in a form that can be readily absorbed. There were no differences in the intestinal Mg concentrations between the calves that received the different rations when expressed as milligrams/gram feed ingested.

The concentration of Na in intestinal contents is given in Table VII. There were no differences in the concentration of Na in the rumen of the calves fed the different rations when expressed as milligrams/gram

TABLE VII

CONCENTRATION OF Na IN INTESTINAL CONTENTS FROM CALVES FED A SEMIPURIFIED, CONCENTRATE, OR CONCENTRATE AND HAY RATION[a]

Item	Semipurified	Concentrate	Concentrate and hay
	mg./gm. feed ingested		
Rumen	15.9 ± 3.3	10.5 ± 3.3	12.3 ± 3.7
Omasum[b]		2.0 ± 0.1	3.6 ± 1.2
Abomasum	15.5 ± 4.8	5.3 ± 3.3	10.3 ± 3.7
SI-1[c]	56.5 ±19.1	41.1 ±20.0	34.9 ±15.2
SI-2	39.2 ± 5.1	26.3 ±10.0	28.0 ± 9.7
SI-3	21.3 ±15.3	13.0 ± 6.0	14.0 ± 5.0
Cecum	4.8 ± 2.9	2.2 ± 0.7	3.7 ± 0.4
LI-1[d]	2.3 ± 2.3	1.1 ± 0.4	2.3 ± 0.6
LI-2	0.7 ± 0.3	0.6 ± 0.3	0.9 ± 0.4
Na in feed (mg./gm.)	12.4	3.0	3.9
Av. daily intake (gm.)	24.5	8.4	9.9

[a]Values expressed as mean ± S.D.

[b]No ingesta in omasum of calves fed the semipurified ration.

[c]SI = small intestine.

[d]LI = large intestine.

of feed ingested. However, the total ruminal Na load was greater in the calves that received the concentrate and hay ration. The average ruminal Na load was 28, 16, and 40 gm. from Groups A, B, and C, respectively. This was largely due to the amount of ingesta in the rumen indicating a more rapid passage of the concentrate ration. This contention is supported by the amount of the unabsorbed markers in the rumen. The average amount of Cr_2O_3 or Ce^{144} in the rumen (expressed as a per cent of the daily dose) was 99, 73, and 103 per cent for Groups A, B, and C, respectively. The greater influx of Na into the rumen of the calves in Groups B and C was probably a consequence of increased rumination on these rations (Table VII, page 43). It is known that Na is absorbed from the rumen (Sperber and Hyden, 1952; and Parthasarathy and Phillipson, 1953), but the quantity of Na in the saliva entering the rumen was greater than the absorption from this organ. Sperber and Hyden (1952) found that Na was absorbed from the rumen against a concentration gradient whereas Parthasarathy and Phillipson (1953) did not demonstrate such Na transport.

There was a large enterosorption of Na into the proximal small intestine. Normally other factors are probably more important in determining the volume and composition of the various secretions entering this region than the daily intake of Na. Absorption occurred throughout the remainder of the tract. In all calves the ingesta reached the cecum before a net loss of Na had occurred from the feed (on the basis of three small intestinal segments). Smith (1962) reported that 40 per cent of the Na intake was absorbed from the ingesta at the distal

small intestine. The per cent of the intake of Na that was absorbed was 94, 80, and 78 per cent for Groups A, B, and C, respectively ($P<.05$, $A > B + C$). The absorption of Na from the small intestine accounted for a much greater percentage of the total Na flux from the gut to the blood than the absorption that occurred in the large intestine. Minimal values of enterosorption or absorption can be obtained by determining the quantity of Na that would have to be insorbed or exsorbed to effect changes from one segment to an adjacent segment.

Assuming that 100 per cent of the unabsorbed marker traversed each segment daily, an average estimate of enterosorption into the proximal small intestine for all calves was 133 gm. Na/day. The values for individual calves ranged from 92-158 gm. Na/day which was approximately 55-60 per cent of the total body Na. However, the actual percentage would be considerably less than this due to recycling. The absorption of Na from the small intestine accounted for 87 per cent of the total Na absorbed from the lower gut. Only 13 per cent of the total Na absorbed from the lower gut was absorbed during passage through the secum and large intestine. The average enterosorption of Na into the gastrointestinal tract was 159 gm. (121-181) per day. The average absorption of Na from the gastrointestinal tract was 168 gm. (128-190) per day.

The K concentrations in the intestinal contents are given in Table VIII. No appreciable changes occurred in the ruminal concentration of K/gram feed ingested of the calves that received the concentrate and concentrate and hay rations. However, an average of 40 per

TABLE VIII

CONCENTRATION OF K IN INTESTINAL CONTENTS FROM CALVES FED A SEMIPURIFIED, CONCENTRATE, OR CONCENTRATE AND HAY RATION[a]

Item	Semipurified	Concentrate	Concentrate and hay
		mg./gm. feed ingested	
Rumen	12.4 ± 6.7	4.2 ± 0.9	6.5 ± 1.8
Omasum[b]		1.7 ± 0.3	2.5 ± 0.5
Abomasum	8.9 ± 4.4	3.0 ± 0.9	3.4 ± 0.3
SI-1[c]	16.4 ± 5.2	17.9 ± 8.7	10.8 ± 6.3
SI-2	9.2 ± 5.8	7.5 ± 2.3	6.7 ± 2.3
SI-3	3.2 ± 1.3	5.7 ± 3.7	3.0 ± 0.7
Cecum	1.3 ± 0.4	2.0 ± 0.3	2.5 ± 0.5
LI-1[d]	0.6 ± 0.2	1.6 ± 0.2	1.8 ± 0.2
LI-2	0.3 ± 0.1	1.1 ± 0.5	1.0 ± 0.5
K in feed (mg./gm.)	20.2	4.2	7.8
Av. daily intake (gm.)	39.0	11.8	25.8

[a]Values expressed as mean ± S.D.

[b]No ingesta in omasum of calves fed the semipurified ration.

[c]SI = small intestine.

[d]LI = large intestine.

cent of the ingested K was absorbed from the rumen of the calves that received the semipurified ration. Sperber and Hyden (1952) reported that the ruminal K concentration was five times that in the plasma suggesting that this element could diffuse across the ruminal epithelium. The apparent absorption of K from the rumen of the calves on the semipurified ration was probably due to the greater concentration gradient resulting from the higher K concentration in the feed. Minimal values of enterosorption or absorption of K were obtained as was done previously for Na. An average enterosorption of 36 gm. (15-45) of K/day occurred in the proximal small intestine. It was also estimated that an average of 36 gm. (15-55) of K was absorbed from the small intestines daily and an average of 4.0 gm. (2.5-5.0) was absorbed from the cecum and large intestines daily. No differences were observed that could be attributed to the type of ration. The concentration of K in the gut appeared to be least affected by its concentration in the feed consumed than any of the other minerals that were measured. This was probably due to the translocation of K from the rumen to the urine. The greater K intake of the calves that received the semipurified ration was excreted in the urine. It is noteworthy that the K concentration in the contents from the proximal small intestine of Group A did not attain the level that was initially present in the ration even with the rather large enterosorption of K that occurred in this region. The per cent of K intake that was absorbed was 98, 75, and 80 per cent for Groups A, B, and C, respectively. The lower values for both Na and K absorption in Groups B and C may be a consequence of the higher fiber content of these rations which

impaired absorption in the large intestine. It is possible that the physical bulk of the undigested residues shielded the Na or K from coming into contact with absorptive surfaces in this area (Mraz and Patrick, 1957).

The total nitrogen concentration in the intestinal contents is given in Table IX. There was a disappearance of N from the rumen of the calves that received the semipurified ration. Few changes were evident in ruminal N concentration of calves in Groups B and C. Errors that may arise from sampling of ruminal contents have previously been noted. Certainly some ruminal disappearance of N should have been observed in Groups B and C. A large, highly variable, enterosorption of N occurred in the proximal small intestine of all calves. Absorption of N occurred throughout the small intestine with no further changes observed in the large intestine. These results would be more meaningful if the origin of the nitrogen was determined. It is known that the total nitrogen in the ingesta is contributed by five general sources: (1) protein from secretions and feed, (2) cellular proliferation of the intestinal mucosa, (3) desquamated cells in pancreatic secretions, (4) nonprotein nitrogen, and (5) bacteria. The intestinal N concentrations leave much to be desired until simplified techniques are available to determine the contribution from each source.

II. IN VIVO EXPERIMENTS

Ileal and jejunal insorption of Ca^{45}, Sr^{89}, Na^{24}, and K^{42} in calves. The first experiment consisted of comparing the insorption of

TABLE IX

CONCENTRATION OF N IN INTESTINAL CONTENTS OF CALVES FED A SEMIPURIFIED, CONCENTRATE, OR CONCENTRATE AND HAY RATION[a]

Item	Semipurified	Concentrate	Concentrate and hay
	mg./gm. feed ingested		
Rumen	26.9 ± 3.5	29.1 ± 9.1	22.5 ± 1.6
Omasum[b]		31.1 ± 4.8	18.0 ± 2.5
Abomasum	35.1 ± 13.4	36.0 ± 15.5	23.5 ± 7.0
SI-1[c]	133.9 ± 46.8	164.6 ± 32.8	94.1 ± 14.6
SI-2	66.4 ± 30.6	76.5 ± 19.1	47.2 ± 17.8
SI-3	19.6 ± 7.2	34.4 ± 24.5	13.1 ± 2.5
Cecum	11.4 ± 5.3	12.0 ± 1.3	8.6 ± 0.2
LI-1[d]	7.8 ± 1.0	11.9 ± 1.6	8.4 ± 1.7
LI-2	7.1 ± 1.8	11.1 ± 0.6	8.4 ± 0.3
N in feed (mg./gm.)	36.9	20.1	20.4
Av. daily intake (gm.)	71.2	57.1	68.1

[a]Values expressed as mean ± S.D.

[b]No ingesta in omasum of calves fed the semipurified ration.

[c]SI = small intestine.

[d]LI = large intestine.

Ca^{45}, Sr^{89}, Na^{24}, and K^{42} from jejunal and ileal preparations. The exact location of the isolated segments was determined after sacrifice. One preparation was approximately 40-45 per cent of the way along the small intestine, henceforth, designated as the jejunum. Since there is no sharp demarcation between the jejunum and ileum in this region the nomenclature is somewhat arbitrary. The ileal preparation was approximately 1 meter cranial to the cecum. The length of the isolated setments averaged 30 cm. (jejunal) and 60 cm. (ileal). The cation concentration of the solutions injected into these two regions was estimated from the intestinal contents of the calves in the first experiment. The volume injected into the lumen ranged from 25-60 ml. depending on the length of the isolated segment.

The blood flow through the jejunal and ileal preparations is given in Table X. There was little difference between the blood flow through the jejunal and ileal preparations. However, the blood flow through the jejunal preparations tended to be greater. Visual examination of the two areas suggests that under normal conditions the blood flow per unit intestine is greater through the jejunum than it is through the ileum. The large variation in blood flow through the preparations was probably intrinsic to the preparation and the physiological state of the animal. It was evident that upon insertion of a polyethylene tube into the vein the inner diameter of the tube could not be matched with the diameter of the vein. Also the elasticity and resistance in the polyethylene tubes was probably different from that in the vein. The summation of the above factors usually produced a slight

TABLE X

BLOOD FLOW THROUGH ISOLATED JEJUNAL AND ILEAL SEGMENTS OF CALVES[a]

Consecutive 30 ml. blood samples	Jejunum[b]	Ileum[c]
	ml./min./gm. ashed intestine	
1	26 ± 9	21 ± 5
2	22 ± 2	21 ± 6
3	24 ± 7	21 ± 7
4	24 ± 8	21 ± 8
5	25 ± 7	23 ± 6
6	19 ± 4	20 ± 7
7	18 ± 4	17 ± 5
8	21 ± 5	20 ± 7
9	23 ± 4	18 ± 5
10	26 ± 6	16 ± 5
11	30 ± 9	19 ± 7
12	29 ± 9	17 ± 5

[a]Values expressed as mean ± S.E.

[b]Observations from seven calves.

[c]Observations from eight calves.

venous obstruction as indicated by the arteriovenous difference in hematocrit values. The venous hematocrit values were 1.5 per cent higher than the arterial values in the preparations that were considered the most desirable.

The insorption of Ca^{45} and Sr^{89} from the isolated jejunal segments is given in Table XI. These values are expressed as per cent dose/milliliter blood/gram ashed intestine $X(10^{-3})$. The intestinal ash was found to be proportional to the serosal surface area of the isolated segments. Therefore, expressing the electrolyte insorption on a per gram intestinal ash basis may have been more accurate than a routine measurement of serosal area. The average was 48.3 (Ca^{45}) and 23.4 (Sr^{89}) for each milliliter of blood collected from the jejunal preparations. The average Sr^{89}/Ca^{45} ratio was 0.47. There was a tendency for the Sr^{89}/Ca^{45} ratio to decrease with time after initiation of the experiment.

The insorption of Ca^{45} and Sr^{89} from the isolated ileal setments is given in Table XII. These values are expressed as per cent dose/milliliter blood/gram ashed intestine $X(10^{-5})$. The average was 98.6 (Ca^{45}) and 74.5 (Sr^{89}) for each milliliter of blood collected from the ileal preparations. The Sr^{89}/Ca^{45} ration averaged 0.76 and did not decrease as markedly in the samples from the ileum as it did from the jejunum.

Upon cursory examination it appears that the insorptive rate for calcium and strontium was much greater in the jejunum than in the ileum. When consideration is given to the difference in calcium concentration in the solutions placed in the lumen the observed insorptive differences

TABLE XI

INSORPTION OF Ca^{45} AND Sr^{89} FROM ISOLATED JEJUNAL SEGMENTS OF CALVES[a]

Consecutive 30 ml. blood samples	Ca^{45}[b]	Sr^{89}[b]	Sr^{89}/Ca^{45}
	% dose/ml. blood/gm. ashed intestine X(10^{-3})		
1	20 ± 9	14 ± 7	0.70
2	29 ± 9	15 ± 5	0.52
3	36 ± 9	17 ± 5	0.47
4	50 ± 14	26 ± 8	0.52
5	53 ± 12	28 ± 9	0.53
6	57 ± 13	27 ± 6	0.47
7	69 ± 19	31 ± 7	0.45
8	54 ± 11	29 ± 8	0.54
9	66 ± 14	34 ± 9	0.51
10	44 ± 8	21 ± 4	0.48
11	50 ± 12	20 ± 3	0.40
12	51 ± 14	19 ± 3	0.37

[a]Values expressed as mean ± S.E.

[b]Observations from seven calves.

TABLE XII

INSORPTION OF Ca^{45} AND Sr^{89} FROM ISOLATED ILEAL SEGMENTS OF CALVES

Consecutive 30 ml. blood samples	Ca^{45}[b]	Sr^{89}[b]	Sr^{89}/Ca^{45}
	% dose/ml. blood/gm. ashed intestine		X(10^{-5})
1	32 ± 12	28 ± 10	0.88
2	71 ± 23	51 ± 17	0.72
3	78 ± 26	67 ± 19	0.86
4	92 ± 31	65 ± 19	0.71
5	85 ± 17	62 ± 19	0.73
6	98 ± 34	72 ± 25	0.73
7	116 ± 36	89 ± 26	0.77
8	112 ± 34	85 ± 26	0.76
9	120 ± 40	91 ± 30	0.76
10	132 ± 39	98 ± 31	0.74
11	115 ± 38	89 ± 31	0.77
12	132 ± 45	97 ± 38	0.73

[a]Values expressed as mean ± S.E.

[b]Observations from eight calves.

become much smaller. The insorption was 15.9 (Ca^{45}) and 10.2 (Sr^{89}) times greater in the jejunum than in the ileum if the calcium was equally effective in diluting Ca^{45} and Sr^{89} in both regions. The underlying assumption is that in both regions the insorption of calcium was nearly proportional to the concentration of calcium in the lumen and that saturation of the calcium insorptive mechanism did not occur. This is not the total explanation as normally the effective time for absorption to occur is greater in the ileum than in the jejunum (Appendix Tables XX-XXII). When the difference in residence time of the ingesta in the two regions under study is taken into consideration, Ca^{45} would normally be insorbed approximately 5.7 and Sr^{89} 3.7 times more rapidly per unit intestine in the jejunum than in the ileum.

The larger Sr^{89}/Ca^{45} ratio in the ileum compared to the jejunum in the calf may be similar to what has been reported with everted intestinal loops from rats. Wasserman (1960) reported Sr/Ca ratios of 0.33 in duodenal segments and 0.57 in ileal segments. Greater discrimination between Ca and Sr in the duodenum was the result of "active" transport of Ca from the mucosal to the serosal surface. It has been reported that the Sr/Ca discrimination factor is constant throughout the entire alimentary tract of rats in vivo (Marcus and Wasserman, 1965). The difference in Sr/Ca ratio observed in this study (jejunum vs. ileum) probably indicates that some transport system involved in Ca absorption does not operate at the same capacity in the ileum as it does in the jejunum. However, the total effective absorptive time is greater in the ileum and this factor allows the ileal region to be very important in

determining over-all Ca and Sr metabolism.

The insorption of Na^{24} and K^{42} from jejunal segments is given in Table XIII. These values are expressed as per cent dose/milliliter blood/gram ashed intestine $X(10^{-3})$. The insorption of Na^{24} appeared to peak at the fifth and sixth blood samples collected and gradually decreased thereafter. This may be similar to the effect Ca ions exert on active Na absorption if it is assumed that removal of the ingesta and preliminary blood flow through the segment reduced the Ca concentration to < 1 mM. at the liminal surface. Dumont et al. (1959) reported that at a Ca concentration of < 1 mM., Ca ions caused a sharp increase in Na insorption from the lumen. The rising phase was interpreted in terms of combination of the divalent cation with the Na carrier system following Michaelis-Menten kinetics. At Ca concentrations greater than 1 mM., the effect of Ca ions was reversed and Na insorption decreased slowly as Ca concentration was increased. The falling phase was ascribed to a non-specific Ca effect which produced a general "stiffening" of the membrane.

The average insorption 94.4 (Na^{24}) and 19.8 (K^{42}) per cent dose/milliliter blood/gram ashed intestine $X(10^{-3})$. The insorption of Na^{24} was approximately 27 times more rapid than the insorption of K^{42} when differences in concentration of Na and K in the jejunal solution were taken into consideration.

The insorption of Na^{24} and K^{42} from the isolated ileal segments is given in Table XIV. These values are expressed as per cent dose/milliliter blood/gram ashed intestine $X(10^{-4})$. The average values are 29.5 (Na^{24}) and 24.8 (K^{42}) for each milliliter of blood collected

TABLE XIII

INSORPTION OF Na^{24} AND K^{42} FROM ISOLATED JEJUNAL SEGMENTS OF CALVES[a]

Consecutive 30 ml. blood samples	Na^{24}[b]	K^{42}[c]
	% dose/ml. blood/gm. ashed intestine X(10^{-3})	
1	30 ± 21	21 ± 13
2	62 ± 20	15 ± 5
3	85 ± 31	14 ± 6
4	120 ± 35	16 ± 5
5	160 ± 45	16 ± 6
6	160 ± 4	18 ± 6
7	116 ± 14	26 ± 6
8	95 ± 17	23 ± 7
9	117 ± 22	27 ± 10
10	69 ± 19	27 ± 9
11	59 ± 13	18 ± 10
12	60 ± 6	17 ± 11

[a]Values expressed as mean ± S.E.

[b]Observations from two calves.

[c]Observations from three calves.

TABLE XIV

INSORPTION OF Na^{24} AND K^{42} FROM ISOLATED ILEAL SEGMENTS OF CALVES[a]

Consecutive 30 ml. blood samples	Na^{24}[b]	K^{42}[c]
	% dose/ml. blood/gm. ashed intestine	X(10^{-4})
1	8 ± 3	11 ± 3
2	10 ± 3	17 ± 3
3	16 ± 1	17 ± 4
4	21 ± 3	19 ± 4
5	26 ± 6	19 ± 4
6	26 ± 5	24 ± 4
7	30 ± 8	27 ± 5
8	36 ± 10	32 ± 5
9	40 ± 13	31 ± 5
10	44 ± 13	33 ± 5
11	46 ± 13	33 ± 5
12	51 ± 14	35 ± 5

[a]Values expressed as mean ± S.E.

[b]Observations from three calves.

[c]Observations from two calves.

through the ileal preparations. The insorption of Na^{24} was approximately seven times more rapid than the insorption of K^{42} when luminal concentration differences are taken into consideration. The insorption of Na^{24} was 32 times greater per unit intestine from the jejunum than from the ileum, whereas the insorption of K^{42} was only 8 times greater from the jejunum than from the ileum. Berger et al. (1959) measured the K flux across canine intestines and cautioned that the K flux may vary considerably across the same tissue under varying conditions. They also reported that 10-100 fold differences should not be considered significant when K fluxes are compared between tissues on the basis of transfer per unit surface area. The greater insorption of Na from both regions probably indicates that its transport mechanism is different from that of K. Also that Na transport, similar to Ca transport, was more rapid in the jejunum than in the distal ileum.

This experiment demonstrated and/or confirmed certain dynamic aspects of gastrointestinal function. Namely: (1) that discrimination against Sr in favor of Ca for insorption is not proportionately constant throughout the gastrointestinal tract of calves, (2) the magnitude of Na and K insorption may change between the jejunum and distal ileum, and (3) the results obtained with Na^{24} and K^{42} insorption from isolated intestinal segments agree with Na and K absorption estimates using unabsorbed markers.

Effects of isomolar replacement of Ca by Sr in the luminal solution upon the relative insorption of Ca^{45} and Sr^{89} in calves. Four calves were used in this experiment and three adjacent jejunal segments

were prepared according to the described procedure. The solutions placed into the lumen contained 5.0 mM. Ca/l., 2.5 mM. Ca/l. and 2.5 mM. Sr/l., and 5.0 mM. Sr/l. The concentrations of the other cations were the same as the jejunal solution given in Table III, page 30. The relative insorption of Ca^{45} and Sr^{89} from the adjacent jejunal segments is given in Table XV. The average Sr^{89}/Ca^{45} ratios were 0.85, 1.50, and 1.98 for the blood collected from the intestinal segments that contained 5.0 mM. Ca/l., 2.5 mM. Ca/l. and 2.5 mM. Sr/l., and 5.0 mM. Sr/l., respectively.

It was known early in studies of Ca and Sr absorption, and is well documented in the literature, that condition(s) and/or factor(s) existed that prevented strontium from traversing the epithelial cell with the same facility as calcium. Cragle and Demott (1959) reported a Sr/Ca ratio of 0.34 from the diet to the blood in dairy cattle--meaning that three times more radiocalcium was transferred than radiostrontium. Mraz (1961) reported similar discrimination in the chick and also that the addition of stable strontium to the diet would not reduce the body burden of radiostrontium. Similar results have been obtained with rats (Hegsted and Bresnagan, 1963). The logical reasoning behind these studies was that stable strontium would dilute the isotope and thereby reduce its absorption and subsequent skeletal deposition. This would be the situation only if the quantity of strontium added to the diet increased the [Sr] in the small intestines above the saturation level (if one exists) for strontium insorption. The precise biochemical and physiological phenomena which determine the magnitude of the differential

TABLE XV

EFFECT OF ISOMOLAR REPLACEMENT OF CALCIUM BY STRONTIUM UPON THE RELATIVE INSORPTION OF Ca^{45} AND Sr^{89} FROM ADJACENT ISOLATED JEJUNAL SEGMENTS OF CALVES[a]

Consecutive 25 ml. blood samples	Composition of solution		
	5.0 mM. Ca/l.[b]	2.5 mM. Ca/l.[b] and 2.5 mM. Sr/l.	5.0 mM. Sr/l.[c]
	% dose Sr^{89}/ml. blood / % dose Ca^{45}/ml. blood		
1	0.85 ± 0.06	1.32 ± 0.14	1.90 ± 0.49
2	0.91 ± 0.07	1.62 ± 0.34	1.94 ± 0.44
3	0.85 ± 0.12	1.36 ± 0.17	2.25 ± 0.66
4	0.82 ± 0.15	1.61 ± 0.25	2.10 ± 0.48
5	0.82 ± 0.16	1.48 ± 0.20	2.02 ± 0.38
6	0.82 ± 0.14	1.47 ± 0.17	1.93 ± 0.38
7	0.83 ± 0.18	1.50 ± 0.15	1.83 ± 0.36
8	0.91 ± 0.21	1.61 ± 0.20	1.88 ± 0.39

[a]Values expressed as mean ± S.E.

[b]Observations from four calves.

[c]Observations from three calves.

transfer of Ca and Sr are unknown, although discrimination has been known to vary under certain conditions, such as the age of the animal and level of calcium in the diet (Comar and Wasserman, 1964; and Thompson, 1963).

The variation observed in this study reinforces the concept that many conditions probably can alter differential Ca and Sr absorption and that absorption of either ion may represent the net effect of a number of absorptive mechanisms. Hence, a single interpretation probably will not satisfactorily explain all the results observed by numerous investigators. A number of possibilities exist that could effect the Sr^{89}/Ca^{45} ratio change that was evident in this study. Unfortunately, the techniques had not attained the necessary refinement to quantitate the effects of luminal Ca and Sr concentrations upon specific Ca^{45} and Sr^{89} insorption. The increase in the Sr^{89}/Ca^{45} ratio observed when Ca was replaced by Sr in the luminal solution would reflect a reduction of Ca^{45} insorption if a competitive relationship is assumed between Ca and Sr ions for insorption (Hendrix et al., 1963). The insorptive Sr^{89}/Ca^{45} ratio should approximate unity at equimolar luminal Ca and Sr concentrations if the relationship was reciprocal. The implications of these results will be discussed later in this chapter.

Effects of hypertonicity upon Ca^{45} and Sr^{89} insorption from adjacent isolated jejunal segments of calves. It is well documented that luminal Ca and Sr concentration may effect the differential transfer of Ca and Sr ions (Wasserman, 1960). The objective of this study was to

determine the effects of hypertonic conditions in the lumen upon Ca and Sr insorption. van Weerden (1961) reported that ingesta in the proximal small intestine of the cow was hypertonic with respect to blood. The hypertonicity in this region was contributed by the organic non-electrolytes. Measurements made on fluid from the proximal small intestinal contents of calves fed the semipurified ration (Experiment 1) were in the range of 360-500 mOs. It is conceivable that under conditions in which a great portion of protein was undergoing hydrolytic breakdown in the proximal small intestine that a hypertonic condition may be produced in the ingesta. However, under normal conditions the intestinal contents are nearly isotonic with blood (Sineshchekov, 1964).

Four calves were used in this experiment and three adjacent jejunal segments were isolated in each calf. The solution injected into the three segments contained 5.0 mM. Ca/l. and the other cations as given in Table III, page 30. The solutions had an osmolality of 288, 383, and 553 mOs., respectively. The osmolality of the solutions was adjusted by the addition of polyethylene glycol to the basal solution. Approximately 50 and 110 gm. of polyethylene glycol/l. was required to increase the osmolality to 383 and 553 mOs., respectively.

The effects of hypertonicity in the lumen upon Ca^{45} insorption from the isolated jejunal segments in given in Table XVI. The results are expressed as per cent dose/milliliter blood/gram ashed intestine $X(10^{-3})$. The observed variation was attributed to variation between the calves attaining different levels of Ca^{45} insorption and in all cases increased osmolality in the lumen produced a reduction in Ca^{45} insorption

TABLE XVI

EFFECT OF HYPERTONICITY IN THE LUMEN UPON THE INSORPTION OF Ca^{45} FROM ADJACENT ISOLATED JEJUNAL SEGMENTS OF CALVES[a]

Consecutive 25 ml. blood samples	Osmolality of solution (mOs.)		
	288[b]	383[b]	553[b]
	% dose/ml. blood/gm. ashed intestine X(10^{-3})		
1	16 ± 5	9 ± 3	4 ± 1
2	40 ± 6	21 ± 6	8 ± 2
3	57 ± 10	31 ± 9	12 ± 3
4	68 ± 13	33 ± 7	21 ± 8
5	76 ± 17	44 ± 12	23 ± 9
6	80 ± 19	42 ± 16	25 ± 9
7	81 ± 17	50 ± 14	30 ± 13
8	91 ± 21	53 ± 18	36 ± 19

[a]Values expressed as mean ± S.E.

[b]Represents observations from four calves.

(Appendix Table XLIV). The insorption of Ca^{45} initially was 53.6 and 21.4 per cent of the Ca^{45} insorption from an isotonic environment for the solutions which had an osmolality of 383 and 553 mOs., respectively. There was equilibration of the luminal solutions with the blood as the Ca^{45} insorption was 59.9 and 38.4 per cent of the isotonic insorption for the 383 and 553 mOs. solutions at the termination of the experiment. Calcium-45 insorption was apparently increased as the liminal solutions became less hypertonic. The average Ca^{45} insorption was 55.7 and 31.3 per cent of the isotonic insorption for the solutions having an osmolality of 383 and 553 mOs., respectively.

The effects of hypertonic conditions in the lumen upon Sr^{89} insorption is given in Table XVII. The average Sr^{89} insorption was 51.4 and 38.5 per cent of the isotonic insorption for the solutions having an osmolality of 383 and 553 mOs., respectively. The insorption of Sr^{89}, similar to Ca^{45} insorption, apparently increased as the luminal solutions became less hypertonic. Initially, the Sr^{89} insorption from the 383 mOs. solutions was 41.9 and increased to 57.3 per cent of the control Sr^{89} insorption by the termination of the experiment. The percentage change was greater for insorption from the 553 mOs. solutions. Initially, the Sr^{89} insorption was 23.3 and increased to 48.9 per cent of the control by the termination of the experiment. A return to isotonicity would have been apparent with little difference in Ca^{45} and Sr^{89} insorption evident between the segments if the experiments were conducted for a longer period of time and the ligated segment could compensate the necessary fluids. The gradual increase in insorption

TABLE XVII

EFFECT OF HYPERTONICITY IN THE LUMEN UPON THE INSORPTION OF Sr^{89} FROM ADJACENT ISOLATED JEJUNAL SEGMENTS OF CALVES[a]

Consecutive 25 ml. blood samples	Osmolality of solution (mOs.)		
	288[b]	383[b]	553[b]
	% dose/ml. blood/gm. ashed intestine X(10^{-3})		
1	13 ± 3	6 ± 1	3 ± 1
2	30 ± 6	12 ± 3	7 ± 3
3	44 ± 11	21 ± 7	12 ± 4
4	54 ± 14	22 ± 6	21 ± 7
5	61 ± 17	34 ± 8	22 ± 9
6	62 ± 18	33 ± 15	23 ± 10
7	63 ± 17	37 ± 13	30 ± 12
8	68 ± 19	38 ± 17	34 ± 17

[a]Values expressed as mean ± S.E.

[b]Represents observations from four calves.

with time (compared to the control segment) is probably an indication that the observed effects represent an osmotic effect rather than a polyethylene glycol effect per se.

The obvious question arises as to what effect hypertonic conditions in the lumen exerted upon differential Ca^{45} and Sr^{89} insorption. The effects of hypertonicity upon the relative insorption of Ca^{45} and Sr^{89} is given in Table XVIII. Little difference was observed in the Sr^{89}/Ca^{45} ratios between the 288 and 383 mOs. solutions as Ca^{45} and Sr^{89} insorption was each reduced about the same magnitude. However, Ca^{45} insorption was decreased more than Sr^{89} insorption from the 553 mOs. solutions. The Sr^{89}/Ca^{45} ratio in the blood draining these segments approached unity or no discrimination against Sr in favor of Ca for insorption was observed. It is known that a metabolically active membrane is necessary before Sr discrimination is observed (Wasserman, 1960). The insorptive Sr^{89}/Ca^{45} ratio (1.0) from the 553 mOs. solutions can be explained by one of, or a combination of, at least two phenomena. Namely: (1) that the transport processes dependent on metabolism were directly affected by luminal hypertonic conditions (553 mOs.) or (2) that observed effects represent a primary effect upon the membrane itself and the loss of "active" or facilitated processes is a consequence of the configuration of the membrane (Kavanau, 1965, 1966).

Effects of altering treatments of isotonic and hypertonic solutions upon the insorption of Ca^{45} and Sr^{89} from the same isolated jejunal segments of calves. Eight calves were utilized in this experiment and the treatments altered according to the design given in

TABLE XVIII

EFFECT OF HYPERTONICITY IN THE LUMEN UPON THE RELATIVE INSORPTION OF Ca^{45} AND Sr^{89} FROM ADJACENT ISOLATED JEJUNAL SEGMENTS OF CALVES

Consecutive 25 ml. blood samples	Osmolality of solution (mOs.)		
	288	383	553
	% dose/Sr^{89}/% dose Ca^{45}		
1	0.81	0.67	0.75
2	0.75	0.57	0.88
3	0.77	0.68	1.00
4	0.79	0.67	1.00
5	0.80	0.77	0.96
6	0.77	0.79	0.92
7	0.78	0.74	1.00
8	0.75	0.72	0.94

NOTE: Values represent averages of four calves.

Table II, page 26. The isolated intestinal preparations were modified to determine the reversibility of the changes observed in the previous two experiments. Both ends of the isolated segment were cut and ligated around tubes (I.D. = 1.25 cm.) to facilitate flushing and changing of the luminal solutions. This preparation made it possible to alter treatments on the same segment. Twenty blood samples (15 ml.) were collected from each treatment. After the first treatment the segments were flushed out with physiological saline. It usually took from 2-4 minutes to accomplish the flushing and the placing the second treatment solution into the lumen. After 20 blood samples were collected from the second treatment, 4×10^{-3} M. iodoacetic acid in aqueous solution was injected into the lumen. Iodoacetate has been shown to be a very effective inhibitor of Ca absorption (Sallis and Holdsworth, 1962). Twenty blood samples were collected after the injection of iodoacetate. It was hoped that this procedure would reduce the variation in Ca^{45} and Sr^{89} insorption observed in the previous experiments as the luminal volume and blood flow for each treatment on the same segment was very similar. The luminal solutions in this experiment all contained 5.0 mM. Ca/l. and had an osmolality of 290 and 396 mOs. The osmolality was adjusted by the addition of polyethylene glycol to the isotonic solution. All values for Ca^{45} and Sr^{89} insorption are expressed as per cent dose/milliliter plasma $X(10^{-3})$. The observed changes in Ca^{45} and Sr^{89} insorption are relative for each calf as the luminal volume was constant (Figures 1-4).

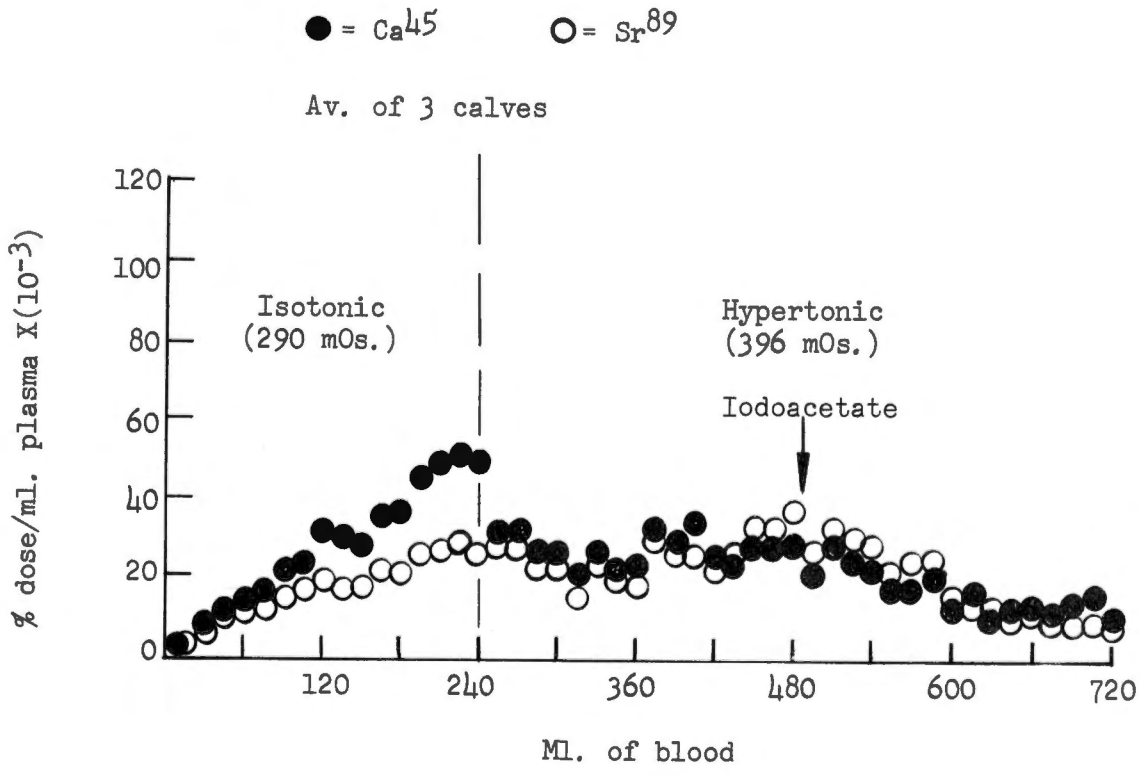

Figure 1. Effects of altering luminal solutions (isotonic ⟶ hypertonic) in the same isolated jejunal segments of calves upon Ca^{45} and Sr^{89} insorption.

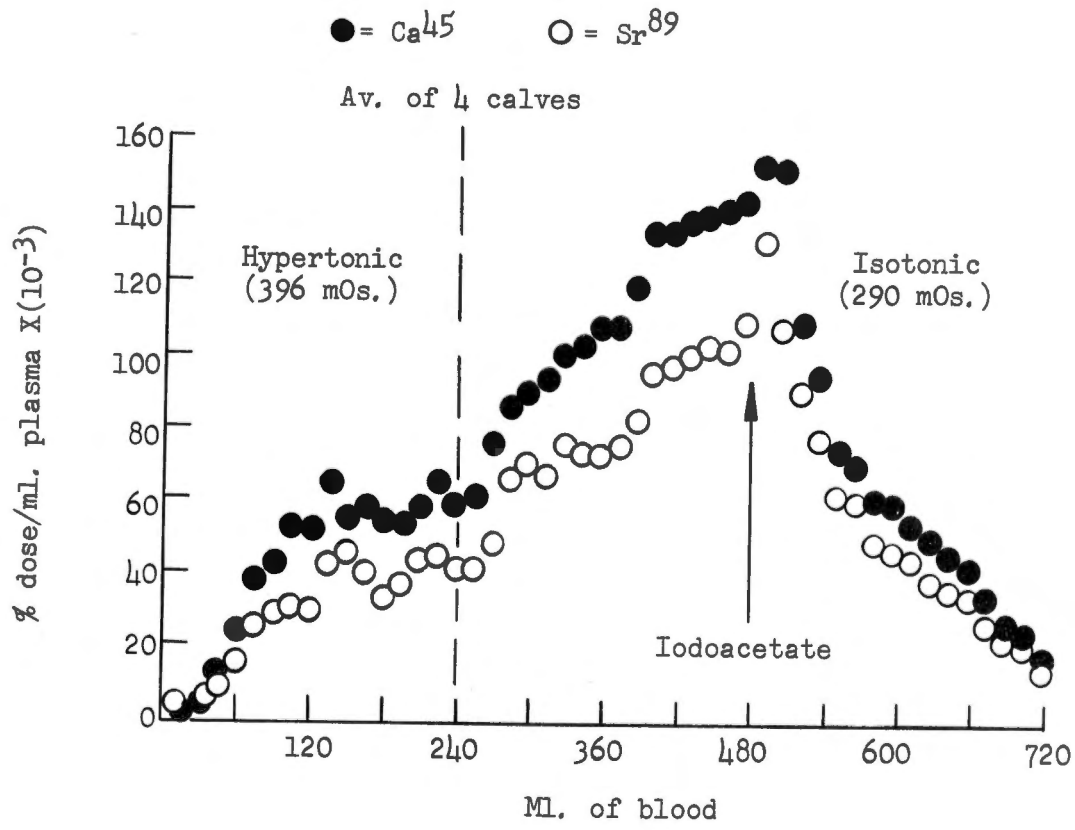

Figure 2. Effects of altering luminal solutions (hypertonic ⟶ isotonic) in the same isolated jejunal segments of calves upon Ca^{45} and Sr^{89} insorption.

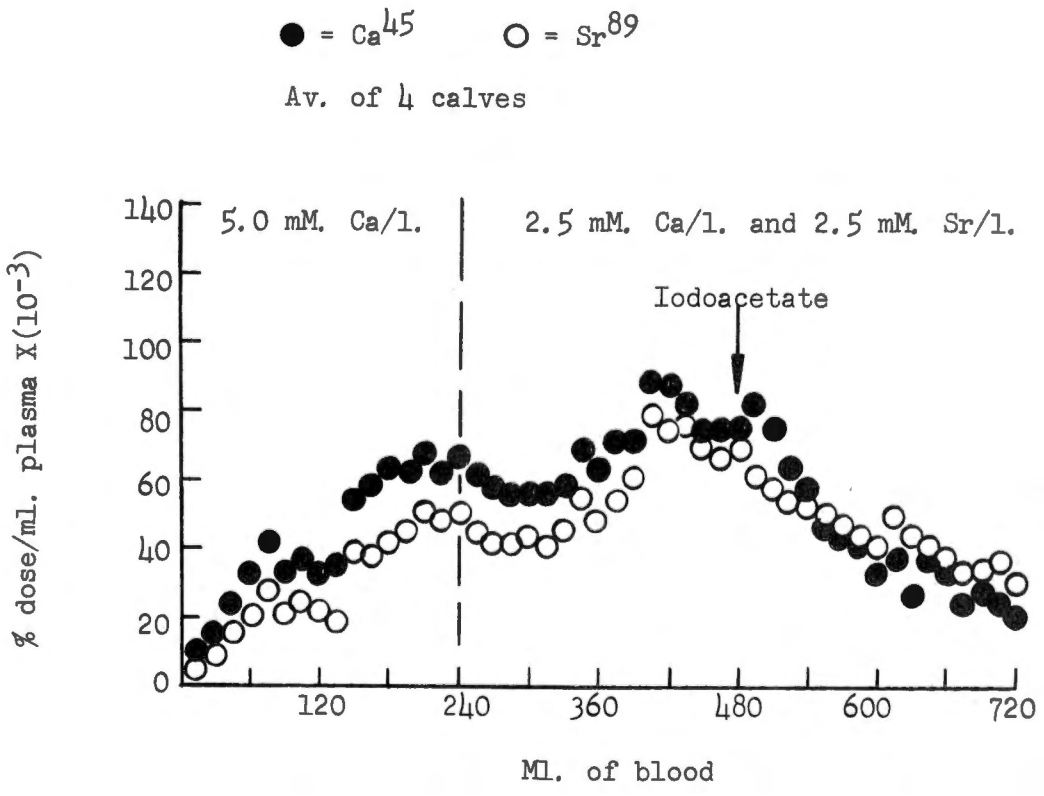

Figure 3. Effects of altering luminal solutions (5.0 mM. Ca ⟶ 2.5 mM. Ca and 2.5 mM. Sr) in the same isolated jejunal segments of calves upon Ca^{45} and Sr^{89} insorption.

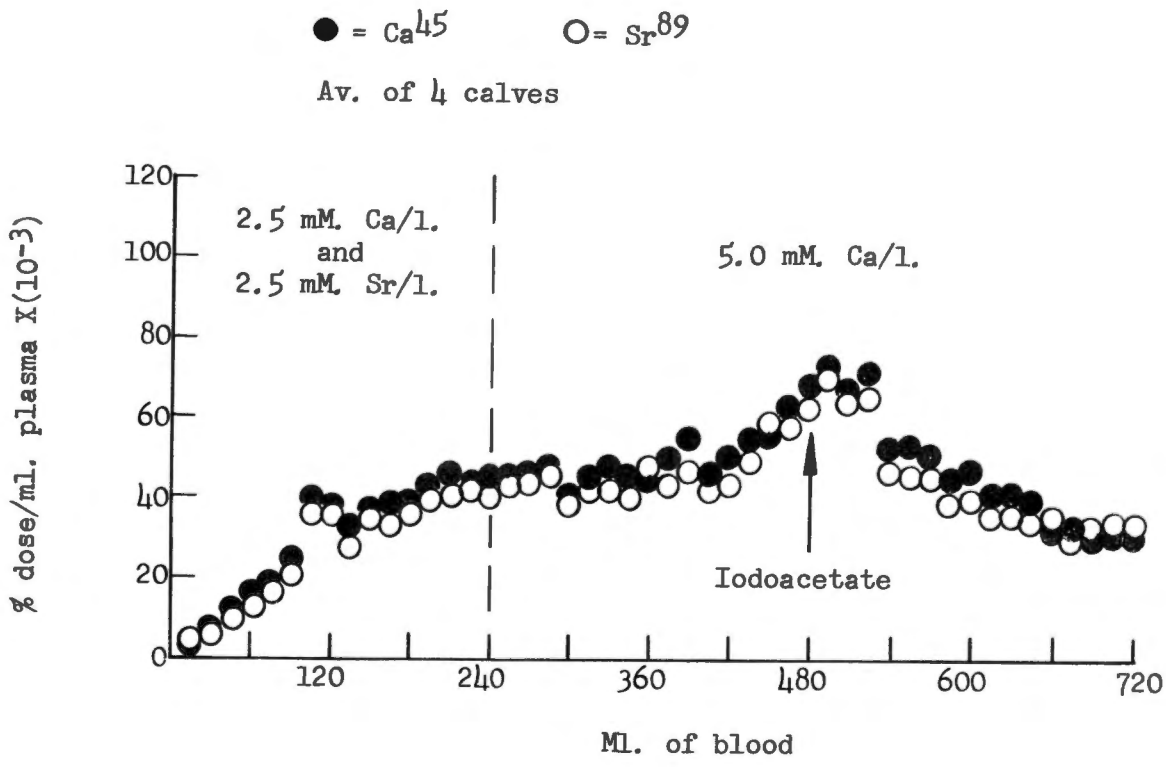

Figure 4. Effects of altering luminal solutions (2.5 mM. Ca and 2.5 mM. Sr $\longrightarrow$ 5.0 mM. Ca) in the same isolated jejunal segments of calves upon Ca^{45} and Sr^{89} insorption.

The average changes in Ca^{45} and Sr^{89} insorption when isotonic solutions were followed by hypertonic solutions in the lumen is given in Figure 1, page 70. There was a gradual decrease in the blood Sr^{89}/Ca^{45} ratio with the number of samples collected when an isotonic solution was in the lumen. The Ca^{45} insorption was decreased to the Sr^{89} isotonic insorptive level upon introduction of the hypertonic solution into the lumen. Iodoacetate had little effect upon Ca^{45} and Sr^{89} insorption from a hypertonic solution. The Sr^{89}/Ca^{45} insorptive ratio was approximately 1.0 from the hypertonic solutions. The reverse of this experiment in which the hypertonic solutions were followed by isotonic solutions in the lumen is given in Figure 2, page 71. Initially, there was a decrease in the Sr^{89}/Ca^{45} ratio with the number of blood samples collected. The ratio change was still evident after the hypertonic solutions had been replaced by isotonic solutions in the lumen. Calcium-45 and Sr^{89} insorption approached a maximum value after 150 ml. of blood had been collected when hypertonic solutions were in the lumen. An increase in both Ca^{45} and Sr^{89} insorption was clearly evident when the lumen contained the isotonic solutions. Iodoacetate reduced both Ca^{45} and Sr^{89} insorption to < 10 per cent of the pre-injection level. The Sr^{89}/Ca^{45} ratio after injection of iodoacetate did approximate unity.

This study showed that a hypertonic solution in the lumen did not disrupt the cellular integrity of the intestinal epithelium because the observed effects were readily reversible. It also showed that the insorptive processes for both Ca^{45} and Sr^{89} were not as sensitive to iodoacetate when a hypertonic solution as compared to when an isotonic

solution was in the lumen. It is interesting to speculate on whether the effects of Ca^{45} and Sr^{89} insorption from luminal hypertonic solutions is an affect directly on the transport processes or whether the membrane assumed a configuration which did not permit "normal" insorption. An interpretation of this important facet depends primarily upon how the membrane is visualized, particularly, the membrane structure as related to function. The effects of a hypertonic $\longrightarrow$ isotonic media in the lumen and vice versa upon Ca^{45} or Sr^{89} insorption appeared to be immediate. This is in contrast to the experiment in which the [Ca] and [Sr] were altered and a lag period was observed in passage of Ca^{45} and Sr^{89} from lumen to blood (Figures 3 and 4, pages 72 and 73). The lag period probably corresponds to the transport time of either Ca^{45} or Sr^{89}. It then is probable that the plasma membrane of the epithelial cells, when presented with a hypertonic medium in the lumen, assumed a configuration in which "active" or facilitated processes did not occur (Kavanau, 1965, 1966). "Active" or facilitated transport processes apparently were not taking place as Ca^{45} or Sr^{89} insorption from a hypertonic medium was relatively insensitive to iodoacetate. Then the reduction in Ca^{45} and Sr^{89} insorption from a hypertonic medium was primarily an effect upon the membrane and the effect upon transport processes was secondary.

Effects of altering [Ca] and [Sr] in the lumen upon insorption of Ca^{45} and Sr^{89} from the same isolated segments of calves. This study was conducted concurrently with the previous experiment. Isotonic solutions containing 5.0 mM. Ca/l. and 2.5 mM. Ca and 2.5 mM. Sr/l. were altered

on the same isolated jejunal segments. The effects of equimolar concentrations of Ca and Sr following 5.0 mM. Ca/l. in the lumen upon Ca^{45} and Sr^{89} insorption is given in Figure 3, page 72. The decrease in Sr^{89}/Ca^{45} ratio with the number of blood samples collected from the luminal 5.0 mM. Ca/l. treatment was again evident. Upon introduction of the equimolar Ca and Sr solution the blood Sr^{89}/Ca^{45} became approximately 1.0. Iodoacetate reduced Ca^{45} and Sr^{89} insorption to about 14 per cent of the pre-iodoacetate injection level. The reverse of this experiment is given in Figure 4, page 73. The average Sr^{89}/Ca^{45} ratio remained at slightly less than unity throughout the entire experiment. It is probable that if the experiment would have been continued for a longer period of time the blood Sr^{89}/Ca^{45} ratio would have decreased when the 5.0 mM. Ca/l. solution was in the lumen.

Effects of time after preparing the isolated intestinal segments upon the relative insorption of Ca^{45} and Sr^{89}. Isolated jejunal and ileal segments were prepared in two calves as previously described. The only exception that was made from the basic preparation was the mesenteric veins were cannulated 30 minutes after the intestinal segments and associate arteries were ligated. The objective of this study was to determine if the observed decrease in blood Sr^{89}/Ca^{45} ratio was inherent to the preparation or a transport time factor. Both solutions contained 5.0 mM. Ca/l. and were injected into the lumen 30 minutes after the initial preparations were made. The results of this study is given in Table XIX. The average Sr^{89}/Ca^{45} ratio was 1.0 and 1.7 for the jejunal

TABLE XIX

EFFECT OF TIME AFTER PREPARATION UPON THE RELATIVE INSORPTION OF Ca^{45} AND Sr^{89} FROM ISOLATED JEJUNAL AND ILEAL SEGMENTS OF CALVES

Consecutive 15 ml. blood samples	Jejunum	Ileum
	% dose Sr^{89}/ml. plasma / % dose Ca^{45}/ml. plasma	
1	1.60	2.33
2	1.40	2.00
3	0.88	1.88
4	0.82	2.22
5	1.33	1.50
6	1.00	2.00
7	1.05	2.00
8	1.08	1.25
9	1.00	1.25
10	0.95	1.00
11	0.75	1.60
12	0.91	1.55
13	0.90	2.00
14	0.89	1.82
15	0.74	1.54
16	0.92	1.23

NOTE: Values represent averages of two calves.

and ileal segments, respectively. A decrease in Sr^{89}/Ca^{45} ratio with the number of blood samples collected was demonstrated again in this study. This is an indication that the observed decrease was not an effect of the preparation but a difference in transport time between Ca^{45} and Sr^{89} from the gut lumen to the blood. The blood Sr^{89}/Ca^{45} ratio from both the jejunal and ileal segments were higher than previously observed. It is proposed that this may represent a reduction in Ca^{45} insorption possibly as a result of decreased temperature after the 30-minute waiting period.

Effects of [Ca] or [Sr] in the lumen of isolated jejunal segments of calves upon the specific insorption of Ca^{45} and Sr^{89}. The first objective of this experiment was to determine the initial passage of Ca^{45} and Sr^{89} from the lumen to the blood. The volume of the blood samples was reduced to 5 ml. to demonstrate the decrease in the blood Sr^{89}/Ca^{45} ratio with the number of samples collected. The second objective was to determine the insorption of Ca^{45} and Sr^{89} when various concentrations of Ca or Sr were in the luminal solutions. A total of six calves were utilized in this experiment and three or four jejunal preparations were made on each calf. All the luminal solutions were isotonic with respect to blood unless otherwise stated.

The results given in Figure 5 show that initially Sr^{89} is insorbed more readily than in Ca^{45} from both isotonic and hypertonic solutions containing 5.0 mM. Ca/l. The blood Sr^{89}/Ca^{45} ratio is less than 1.0 only after 20-25 ml. of blood was collected. This agrees with

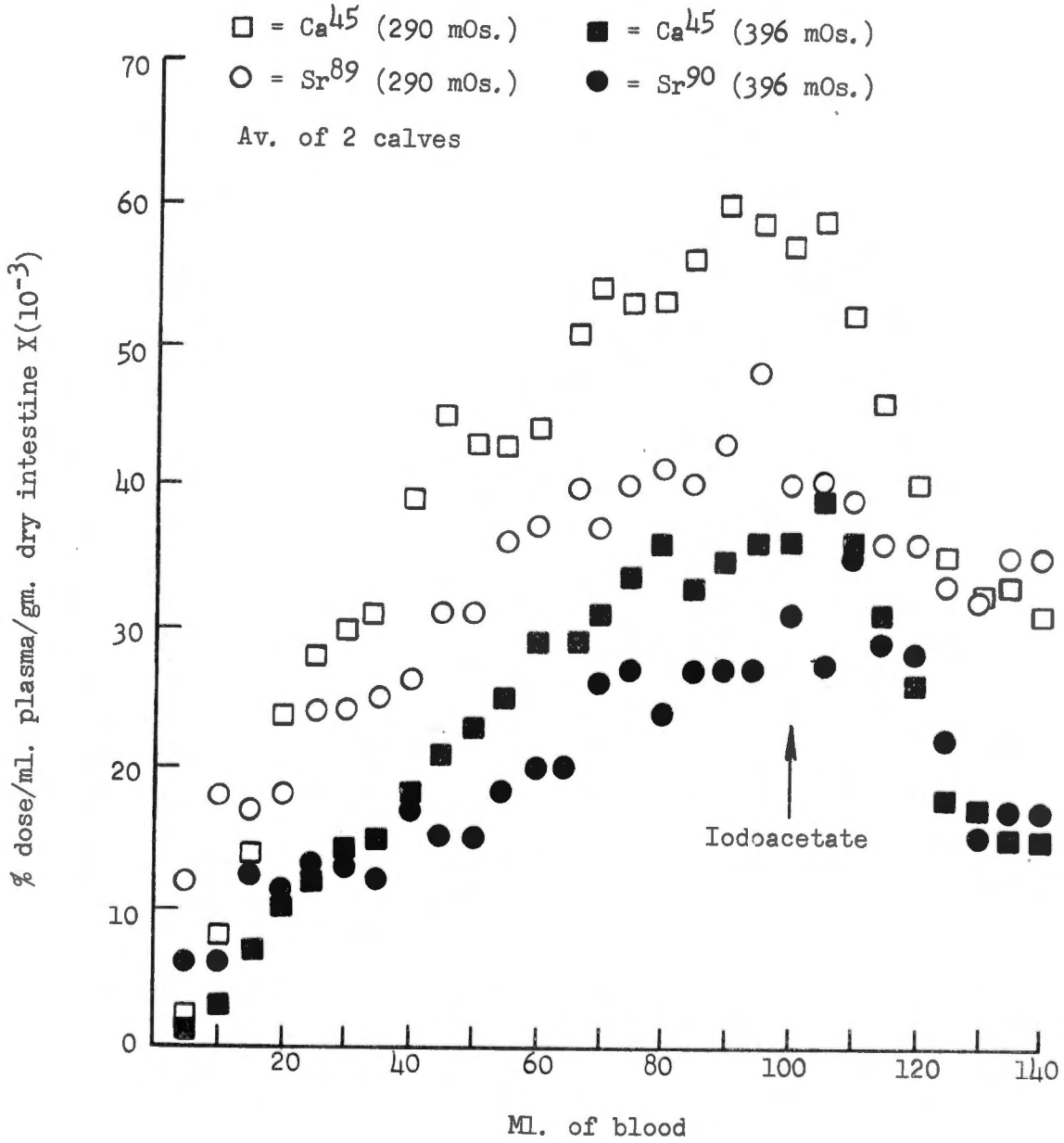

Figure 5. Effects of hypertonic and isotonic solutions in the lumen upon insorption of Ca^{45} and Sr^{89} from isolated jejunal segments of calves.

results obtained from previous experiments in which 15 ml. blood samples were collected. Calcium-45 insorption followed a curvilinear pattern from isotonic luminal solutions and a linear pattern from hypertonic luminal solutions. This is very similar to Ca^{45} insorption from segments containing isotonic solutions that had been previously "poisoned" with iodoacetate (Figure 6). This suggests that "active" or facilitated Ca^{45} insorption was greatly reduced when hypertonic solutions were in the lumen.

It has been reported that calcium always moves more rapidly across the membrane system than does strontium (Comar et al., 1956; Wasserman et al., 1957; and Wasserman et al., 1958). This apparently is not the situation in the initial passage of Ca^{45} and Sr^{89} across the intestinal epithelium of the calf. Corallary results have been obtained in the transfer of Ca^{45} and Sr^{89} across everted intestinal loops of rats (Hendrix et al., 1963) and calves (Perry, 1967). In these studies radiostrontium moved from the mucosal to serosal surfaces with greater facility than radiocalcium. The transfer of radiocalcium was equal to or greater than the transfer of radiostrontium when the amount of each in the tissue was considered to be also transferred. This may indicate a difference in physiological time between in vivo and in vitro procedures and the mucosal to serosal transfer represented only the initial passage. Therefore, more radiostrontium is found in the serosal media than radiocalcium. The differences observed in the initial passage of Ca^{45} and Sr^{89} may also lend support to the two processes involved in Ca absorption as proposed by Schachter (1963).

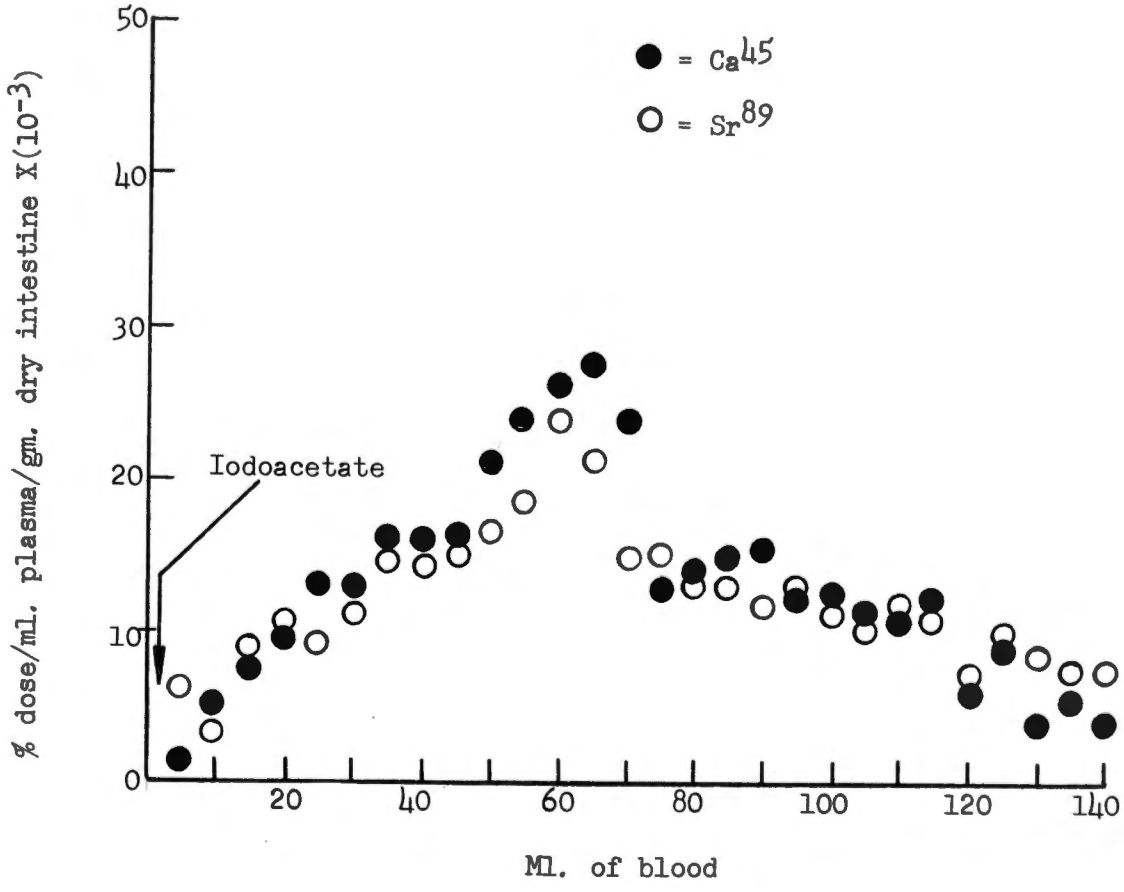

Figure 6. Effects of iodoacetate upon Ca^{45} and Sr^{89} insorption from isolated jejunal segments of calves.

The initial passage of Sr^{89} may represent the insorption that occurs by simple diffusion and/or exchange mechanisms. This is supported by the finding that at no time after iodoacetate injection is the Sr^{89} insorption depressed below the level of insorption after 3-5 samples of blood had been collected. The increase above the initial leveling off is apparently the Sr^{89} insorption that is sensitive to iodoacetate and would not be consistent with a simple diffusion mechanism. The extent of the added contribution of the iodoacetate-sensitive mechanism may account for a portion of the variation in Sr^{89} insorption observed in these studies.

This contention is supported, to some extent, by the results given in Figure 7. These were two calves of approximately the same size and receiving similar rations and a great difference was observed in the comparative insorption of Ca^{45} and Sr^{89}. The same solutions were used in both calves and contained 10 mM. Ca/l. The insorption of Ca^{45} and Sr^{89} in calf 30 was approximately what is usually obtained under these conditions (Sr^{89}/Ca^{45} = 0.30). The results from calf 29 were much different as the Sr^{89} insorption was much greater than the Ca^{45} insorption. It is easy to visualize Ca^{45} insorption fluctuating independently of Sr^{89} insorption if an "active" or facilitated mechanism is assumed for calcium insorption. However, fluctuation of Sr^{89} insorption which may be independent of Ca^{45} insorption is difficult to interpret (calf 29, Figure 7). One explanation may be the interplay of a strontium-specific insorptive mechanism that is sensitive to iodoacetate. Another explanation may be that in the calf that responded

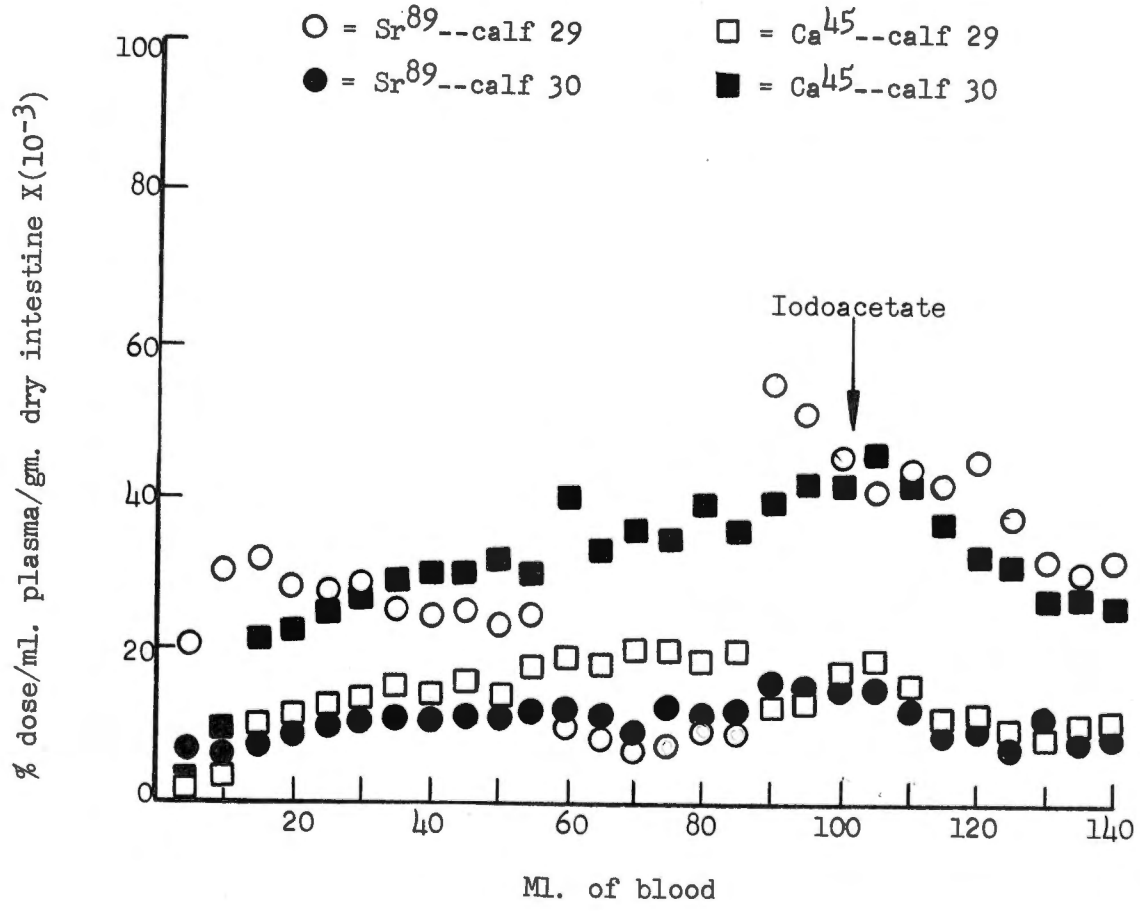

Figure 7. Insorption of Ca^{45} and Sr^{89} from isolated jejunal segments of calves containing 10 mM. Ca/l.

"normally" (calf 30) the rate-limiting step in insorption was the initial penetration of calcium and strontium through the diffusion barrier (Harrison and Harrison, 1960). The variation in Ca^{45} and Sr^{89} insorption (Sr^{89}/Ca^{45} ratio > 1.0) observed in calf 29 may occur if the rate-limiting step in Ca^{45} insorption was the actual transport of Ca^{45} to the blood. Schachter et al. (1966) have shown that both processes involved in calcium absorption may be rate-limiting depending upon the conditions at the time of measurement.

The effects of luminal [Ca] or [Sr] upon the specific insorption of Ca^{45} and Sr^{89} are given in Figures 8 and 9. These results are expressed as per cent dose insorbed per milliliter plasma per gram dry intestine $X(10^{-3})$. The plasma flow through the isolated intestinal preparations was very similar and averaged 2.1 ml. per minute per gm. dry intestine. It is shown in Figure 8 that the Ca^{45} insorption from segments whose luminal solutions contained 5.0 mM. and 10.0 mM. Ca/l. was approximately the same. This is important because it demonstrates that at the [Ca] studied, Ca^{45} insorption was proprotional to the [Ca] in the lumen and that saturation of the Ca insorptive mechanism was not attained. It is also evident that the Ca^{45} insorptive mechanism is somewhat specific as Ca^{45} insorption from solutions containing 1 mM. and 5 mM. Sr/l. was greater than from the solutions containing Ca. The results of Ca^{45} insorption in this study (Figure 8) would be consistent with the hypothesis that the rate-limiting step in calcium insorption was the penetration of the diffusion barrier at the mucosal surface. These data may also be interpreted that in the penetration of the

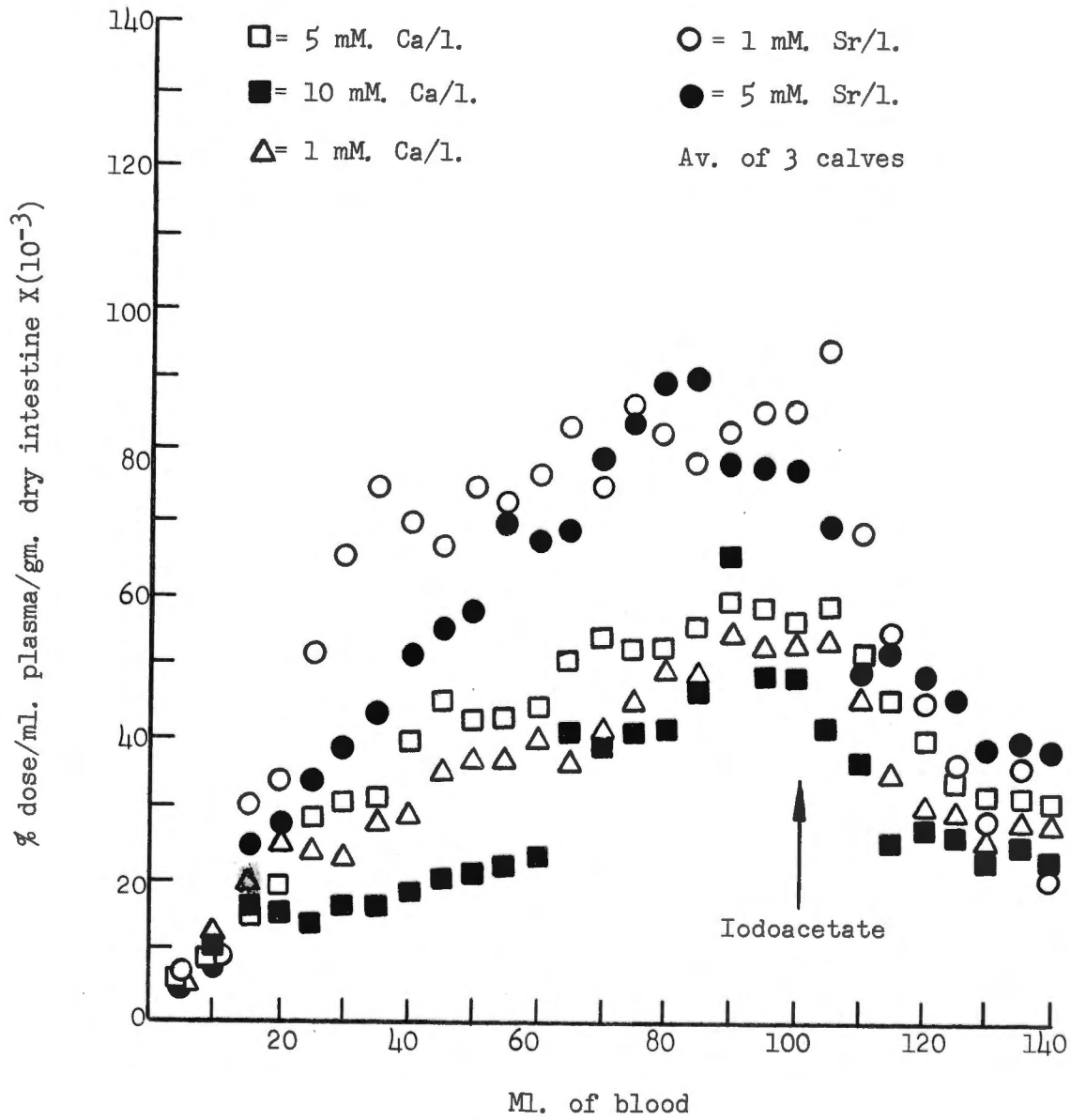

Figure 8. Insorption of Ca^{45} from isolated jejunal segments of calves containing various concentrations of Ca or Sr in the lumen.

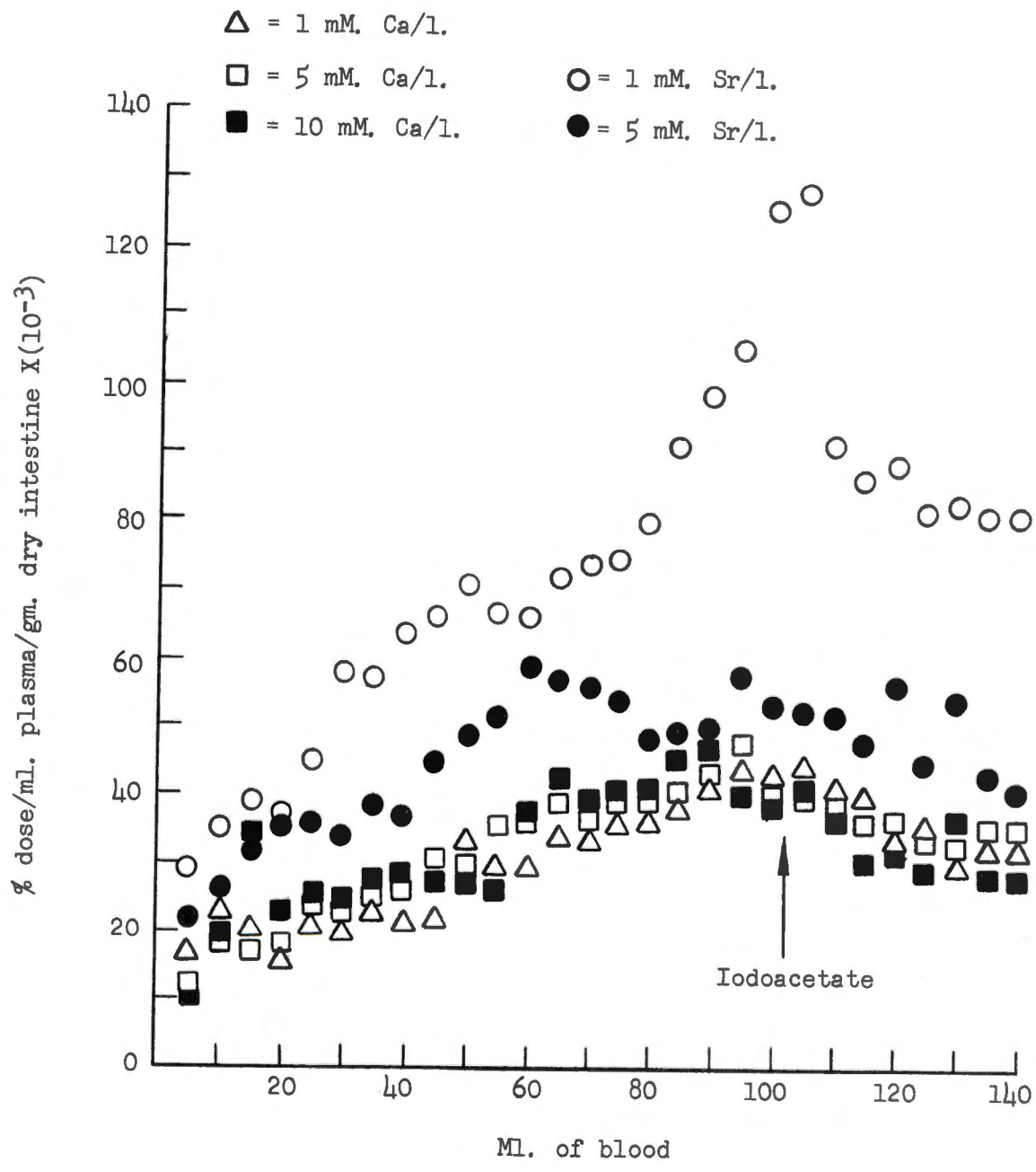

Figure 9. Insorption of Sr^{89} from isolated jejunal segments of calves containing various concentrations of Ca or Sr in the lumen.

mucosal diffusion barrier that Ca and Sr ions behave similarly. More Ca^{45} is transferred from the lumen to the blood because of its more rapid transport rate.

The results of Ca^{45} insorption are similar to Ca absorption data obtained by Cramer (1963) with Thiry-Vella fistula's in dogs. Although Ca insorption was not studied over the necessary $[Ca]$, preliminary examination indicates that these data may conform to Michaelis-Menten kinetics. Conformation to Michaelis-Menten kinetics suggests that calcium insorption is not due solely to passive diffusion but utilizes a carrier system with the character of facilitated transport system and with a limited capacity (Cramer, 1963). Schachter et al. (1966) postulated that the penetration of the mucosal barrier may involve facilitated diffusion and that the second process involves active transport. However, if the rate-limiting step in Ca insorption was the mucosal barrier the entire process would have the character of facilitated diffusion. The sensitivity of Ca^{45} insorption to iodoacetate throughout these studies does not necessarily indicate an active transport system. Laster and Ingelfinger (1961) suggested that both active transport and facilitated transport may involve carrier systems and may be variants of the same process. They differ chiefly in that the latter does not require metabolic energy. However, active transport and facilitated diffusion may be inhibited by the same type of substances (Danielli, 1958). It is easier to visualize physiologic control over calcium absorption if a transport mechanism is involved rather than merely physical diffusion. Cramer (1963) concluded that calcium

absorption in dogs occurs by facilitated transort and may be modified to meet the need of the body.

Strontium-89 insorption from segments containing various Ca or Sr concentrations is given in Figure 9, page 86. Interestingly, Sr^{89} insorption appeared to be greater when the luminal solutions contained Sr than when they contained Ca. However, it should be emphasized that insorption from isolated intestinal segments is often difficult to quantitate. Iodoacetate decreased Ca^{45} insorption but had little effect upon Sr^{89} insorption. This reinforces the concept that the initial penetration of the mucosal barrier may have been the rate-limiting step in both Ca^{45} and Sr^{89} insorption. Then it may be assumed that it is the second process in Ca insorption that is sensitive to iodoacetate. It can be interpreted that penetration of the mucosal barrier is the limiting factor when iodoacetate had no effect upon Sr^{89} insorption and the Sr^{89}/Ca^{45} ratio was unity after iodoacetate inhibition. A Sr^{89}/Ca^{45} ratio < 1.0 prior to iodoacetate injection reflects the rapidity of Ca^{45} transfer and the similar behavior of Ca and Sr ions in penetrating the mucosal barrier. A possibility exists that Sr ions would compete more favorably for an otherwise Ca-specific transport system if an increase in cellular $[Sr]$ resulted when only Sr was in the luminal solution. This may then effect an increase in Sr^{89} insorption.

CHAPTER V

SUMMARY

Eleven calves were utilized to determine the effects of semi-purified, concentrate, or concentrate and hay rations upon the enterosorption or absorption of Ca, Mg, Na, K, and N. Unabsorbed markers (Cr_2O_3 or Ce^{144}) were used to determine the net exchanges of the above constituents at various locations along the gastrointestinal tract. An enterosorption of Ca, Mg, Na, K, and N occurred in the proximal small intestines of all calves. Absorption of these constituents was greatest in passage through the small intestines. Few differences (expressed as milligrams per gram feed ingested) attributable to ration were observed in the small intestines. It appeared that the exsorption of electrolytes into the gut was relatively independent of the quantities ingested under the conditions of this study.

The insorption of Ca^{45} and Sr^{89} was studied in 32 young calves using isolated intestinal segments in vivo. The insorption of Ca^{45} and Sr^{89} was more rapid from jejunum than from the ileum. The average Sr^{89}/Ca^{45} ratio in the blood draining the jejunal and ileal segments was 0.47 and 0.76, respectively.

Mildly hypertonic solutions (383 mOs.) in the lumen reduced Ca^{45} and Sr^{89} insorption (compared to insorption from an isotonic media) but the same blood Sr^{89}/Ca^{45} ratio was maintained. However, when hypertonic solutions (553 mOs.) was in the lumen Ca^{45} insorption was reduced more

than Sr^{89} insorption and the blood Sr^{89}/Ca^{45} ratio approximated unity. The observed differences in Ca^{45} and Sr^{89} insorption from isotonic and hypertonic luminal solutions appeared to be readily reversible.

The blood Sr^{89}/Ca^{45} was also affected by the [Ca] or [Sr] in the lumen. The average blood Sr^{89}/Ca^{45} ratios were 0.85, 1.50, and 1.98 from isolated segments that contained 5.0 mM. Ca, 2.5 mM. Ca and 2.5 mM. Sr, and 5.0 mM. Sr per liter. A decrease in the blood Sr^{89}/Ca^{45} ratio was observed with the number of samples collected when the luminal solution contained 5.0 mM. Ca per liter. Further studies demonstrated that the initial passage of Sr^{89} from the lumen to the blood is more rapid than that of Ca^{45} and accounted for the observed decrease in blood Sr^{89}/Ca^{45} ratio.

Attempts were made to determine the effects of luminal [Ca] or [Sr] upon the specific insorption of Ca^{45} and Sr^{89}. It was demonstrated that Ca^{45} insorption was proportional to the [Ca] in the lumen when the luminal solution contained 5.0 or 10.0 mM. Ca per liter. The insorption of Ca^{45} was increased when the luminal solutions contained 1.0 or 5.0 mM. Sr per liter illustrating the specificity of the calcium insorptive mechanism. The implications of these data were discussed with regard to relative Ca^{45} and Sr^{89} insorption.

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APPENDIX

TABLE XX

INTESTINAL DISTRIBUTION OF Ce^{144} IN CALVES FED SEMIPURIFIED RATIONS

Section of G.I. tract	Calf no. 99-	360	365	371	Av.	% of total
	% of daily dose					
Rumen	85.5	117.0	125.3	70.1	99.4	60.7
Omasum[a]						
Abomasum	3.6	4.3	3.2	2.8	3.5	2.1
SI-1[b]	0.5	0.1	0.6	0.3	0.4	0.2
SI-2	1.7	2.5	1.0	0.6	1.5	0.9
SI-3	1.7	0.7	2.2	0.2	1.2	0.7
SI-4	1.5	3.2	3.5	0.1	2.1	1.3
SI-5	3.7	7.1	0.3	2.3	3.5	2.1
SI-6	3.0	4.1	3.7	5.0	4.0	2.4
Cecum	16.8	14.9	16.2	10.8	14.7	9.0
LI-1[c]	2.8	3.4	11.6	18.2	9.0	5.5
LI-2	12.6	39.8	13.5	32.0	24.5	15.1
TOTAL	133.4	197.1	181.1	142.4	163.8	100.0

[a]No ingesta in the omasum.

[b]SI = small intestine.

[c]LI = large intestine.

TABLE XXI

INTESTINAL DISTRIBUTION OF Cr_2O_3 IN CALVES FED CONCENTRATE RATIONS

Section of G. I. tract	Calf no. 372	373	377	380	Av.	% of total	
	% of daily dose						
Rumen	70.0	78.8	65.6	75.9	72.6	55.2	
Omasum	29.4	13.4	22.8	15.8	20.4	15.5	
Abomasum	4.1	2.6	3.3	2.4	3.1	2.4	
SI-1[a]	0.4	0.7	0.2	0.3	0.4	0.3	0.6
SI-2	0.4	0.3	0.4	0.3	0.4	0.3	
SI-3	1.2	0.3	0.8	1.3	0.9	0.7	1.4
SI-4	0.7	1.1	0.7	1.2	0.9	0.7	
SI-5	0.7	1.9	1.9	1.0	1.4	1.1	2.6
SI-6	0.8	3.4	2.4	1.5	2.0	1.5	
Cecum	4.7	3.9	8.3	9.0	6.5	4.9	
LI-1[b]	8.3	17.7	9.8	10.9	11.7	8.9	
LI-2	10.9	11.9	10.6	11.3	11.2	8.5	
TOTAL	131.6	136.0	126.8	130.9	131.5	100.0	

[a]SI = small intestine.

[b]LI = large intestine.

TABLE XXII

INTESTINAL DISTRIBUTION OF Ce^{144} IN CALVES FED CONCENTRATE AND HAY RATIONS

Section of G.I. tract	Calf no. 291	Calf no. 362	Calf no. 370	Av.	% of total
			% of daily dose		
Rumen	104.9	106.6	97.3	102.9	58.1
Omasum	16.9	21.1	30.3	22.8	12.9
Abomasum	4.4	0.7	5.1	3.4	1.9
SI-1[a]	0.1	1.1	0.4	0.5	0.3
SI-2	0.7	0.6	0.1	0.4	0.2
SI-3	1.0	2.3	1.8	1.7	1.0
SI-4	1.1	1.9	1.7	1.6	0.9
SI-5	2.5	4.7	1.1	2.8	1.6
SI-6	4.1	4.0	5.6	4.6	2.6
Cecum	12.1	14.0	8.5	11.5	6.5
LI-1[b]	6.0	12.3	4.4	7.6	4.3
LI-2	23.7	14.9	13.1	17.2	9.7
TOTAL	177.5	184.2	169.4	177.0	100.0

[a]SI = small intestine.

[b]LI = large intestine.

TABLE XXIII

INTESTINAL CONCENTRATIONS OF CALCIUM IN CALVES FED SEMIPURIFIED RATIONS

Section of G.I. tract	Calf no. 99	360	365	371	Av.
	mg./gm. ingesta				
Rumen	0.65	0.58	1.19	0.41	0.71
Omasum[a]					
Abomasum	0.44	0.38	0.65	0.31	0.45
SI-1[b]	0.33	0.38	0.20	0.11	0.26
SI-2	0.24	0.20	0.19	0.13	0.18
SI-3	0.19	0.17	0.29	0.16	0.20
SI-4	0.21	0.18	0.37	0.19	0.24
SI-5	0.24	0.28	0.64	0.32	0.37
SI-6	0.38	0.41	0.17	0.51	0.62
Cecum	0.71	0.95	2.60	1.60	1.47
LI-1[c]	3.81	2.62	3.28	1.52	2.81
LI-2	4.07	4.31	4.77	4.76	4.48

[a]No ingesta in the omasum.

[b]SI = small intestine.

[c]LI = large intestine.

TABLE XXIV

INTESTINAL CONCENTRATIONS OF CALCIUM IN CALVES FED CONCENTRATE RATIONS

Section of G.I. tract	Calf no. 372	373	377	380	Av.
	mg./gm. ingesta				
Rumen	0.32	0.68	0.65	0.23	0.47
Omasum	0.86	0.91	1.36	0.83	0.99
Abomasum	0.99	1.04	0.88	0.71	0.91
SI-1[a]	0.20	0.26	[b]	[b]	0.23
SI-2	0.13	0.17	0.23	0.14	0.18
SI-3	0.31	0.21	0.14	0.24	0.23
SI-4	0.15	0.30	0.13	0.27	0.21
SI-5	0.18	0.53	0.33	0.25	0.32
SI-6	0.68	0.67	0.43	0.32	0.53
Cecum	0.73	1.11	0.51	0.65	0.75
LI-1[c]	1.00	0.99	0.58	0.66	0.81
LI-2	1.07	0.84	0.87	0.82	0.90

[a]SI = small intestine.

[b]No determination.

[c]LI = large intestine.

TABLE XXV

INTESTINAL CONCENTRATIONS OF CALCIUM IN CALVES FED CONCENTRATE AND HAY RATIONS

Section of G.I. tract	Calf no. 291	362	370	Av.
		mg./gm. ingesta		
Rumen	2.04	2.68	2.15	2.29
Omasum	4.67	4.97	4.28	3.48
Abomasum	2.88	3.01	2.62	2.84
SI-1[a]	0.22	0.61	0.33	0.39
SI-2	0.26	0.55	0.31	0.37
SI-3	0.31	0.56	0.48	0.45
SI-4	0.74	0.75	0.69	0.73
SI-5	1.33	1.41	1.45	1.39
SI-6	1.40	1.81	1.56	1.59
Cecum	1.85	3.30	2.48	2.54
LI-1[b]	1.94	3.60	2.87	2.80
LI-2	2.70	4.51	3.79	3.67

[a]SI = small intestine.

[b]LI = large intestine.

TABLE XXVI

INTESTINAL CONCENTRATIONS OF MAGNESIUM IN CALVES FED SEMIPURIFIED RATIONS

Section of G.I. tract	Calf no. 99	360	365	371	Av.
	mg./gm. ingesta				
Rumen	0.18	0.19	0.13	0.22	0.18
Omasum[a]					
Abomasum	0.13	0.14	0.10	0.09	0.12
SI-1[b]	0.16	0.11	0.08	0.17	0.13
SI-2	0.13	0.12	0.08	0.15	0.12
SI-3	0.07	0.10	0.11	0.10	0.10
SI-4	0.11	0.12	0.14	0.16	0.13
SI-5	0.12	0.18	0.22	0.21	0.18
SI-6	0.19	0.26	0.33	0.30	0.27
Cecum	0.32	0.41	0.25	0.59	0.39
LI-1[c]	1.30	0.72	0.56	0.66	0.81
LI-2	0.93	1.12	0.63	1.38	1.02

[a]No ingesta in the omasum.

[b]SI = small intestine.

[c]LI = large intestine.

TABLE XXVII

INTESTINAL CONCENTRATIONS OF MAGNESIUM IN CALVES FED CONCENTRATE RATIONS

Section of G.I. tract	Calf no. 372	373	377	380	Av.
			mg./gm. ingesta		
Rumen	0.41	0.37	0.37	0.25	0.35
Omasum	0.47	0.53	0.79	0.49	0.57
Abomasum	0.26	0.27	0.11	0.11	0.19
SI-1[a]	0.27	0.22	[b]	[b]	0.25
SI-2	0.25	0.23	0.24	0.28	0.25
SI-3	0.31	0.23	0.13	0.25	0.23
SI-4	0.34	0.22	0.14	0.23	0.23
SI-5	0.36	0.33	0.30	0.26	0.31
SI-6	0.51	0.62	0.42	0.32	0.47
Cecum	0.71	0.85	0.61	0.73	0.73
LI-1[c]	0.75	0.90	0.70	0.77	0.78
LI-2	0.83	0.96	0.88	0.81	0.87

[a]SI = small intestine.

[b]No determination.

[c]LI = large intestine.

TABLE XXVIII

INTESTINAL CONCENTRATIONS OF MAGNESIUM IN CALVES FED CONCENTRATE AND HAY RATIONS

Section of G.I. tract	Calf no. 291	362	370	Av.
		mg./gm. ingesta		
Rumen	0.47	0.48	0.39	0.45
Omasum	0.77	0.70	0.71	0.73
Abomasum	0.47	0.48	0.42	0.48
SI-1[a]	0.22	0.26	0.20	0.23
SI-2	0.29	0.24	0.23	0.25
SI-3	0.22	0.21	0.19	0.21
SI-4	0.31	0.26	0.28	0.28
SI-5	0.43	0.38	0.42	0.41
SI-6	0.79	0.41	0.62	0.61
Cecum	0.85	0.72	0.71	0.76
LI-1[b]	0.93	0.75	0.84	0.84
LI-2	1.31	0.97	1.06	1.11

[a]SI = small intestine.

[b]LI = large intestine.

TABLE XXIX

INTESTINAL CONCENTRATIONS OF SODIUM IN CALVES FED SEMIPURIFIED RATIONS

Section of G. I. tract	Calf no. 99	360	365	371	Av.
	mg./gm. ingesta				
Rumen	3.22	2.08	3.41	2.73	2.86
Omasum[a]					
Abomasum	2.50	1.03	2.02	1.48	1.76
SI-1[b]	2.92	2.38	2.95	3.38	2.91
SI-2	3.30	1.80	3.59	3.44	3.03
SI-3	3.01	1.83	3.60	3.45	2.97
SI-4	3.78	2.45	3.55	3.40	3.29
SI-5	3.36	2.96	2.93	3.81	3.27
SI-6	3.18	2.80	2.83	3.48	3.07
Cecum	2.98	1.41	2.08	3.48	2.44
LI-1[c]	1.62	1.59	1.62	3.33	2.04
LI-2	0.75	1.03	1.20	1.73	1.18

[a]No ingesta in the omasum.

[b]SI = small intestine.

[c]LI = large intestine.

TABLE XXX

INTESTINAL CONCENTRATIONS OF SODIUM IN CALVES FED CONCENTRATE RATIONS

Section of G.I. tract	Calf no. 372	373	377	380	Av.
			mg./gm. ingesta		
Rumen	1.25	1.01	1.97	1.38	1.40
Omasum	0.58	0.73	0.67	0.65	0.66
Abomasum	0.37	0.55	0.56	0.69	0.54
SI-1[a]	1.31	1.15	1.74	0.71	1.48
SI-2	1.72	1.77	2.11	1.93	1.88
SI-3	1.79	1.45	2.18	2.23	1.91
SI-4	1.77	1.24	2.44	1.80	1.81
SI-5	1.85	1.65	2.25	1.14	1.72
SI-6	0.89	0.86	2.05	1.59	1.35
Cecum	0.66	0.55	0.92	0.88	0.75
LI-1[b]	0.37	0.40	0.82	0.29	0.47
LI-2	0.21	0.34	0.38	0.10	0.26

[a]SI = small intestine.

[b]LI = large intestine.

TABLE XXXI

INTESTINAL CONCENTRATIONS OF SODIUM IN CALVES FED CONCENTRATE AND HAY RATIONS

Section of G.I. tract	Calf no. 291	362	370	Av.
		mg./gm. ingesta		
Rumen	3.05	2.56	1.58	2.39
Omasum	2.03	1.85	1.30	1.73
Abomasum	1.96	2.00	0.94	1.63
SI-1[a]	2.87	3.03	1.12	2.34
SI-2	3.59	2.59	2.00	2.73
SI-3	3.24	3.06	2.53	2.94
SI-4	4.27	3.07	2.29	3.21
SI-5	2.85	3.22	2.42	3.16
SI-6	3.09	3.27	2.04	2.80
Cecum	1.80	1.62	1.45	1.62
LI-1[b]	0.86	1.14	1.26	1.09
LI-2	0.38	0.50	0.78	0.55

[a]SI = small intestine.

[b]LI = large intestine.

TABLE XXXII

INTESTINAL CONCENTRATIONS OF POTASSIUM IN CALVES FED SEMIPURIFIED RATIONS

Section of G.I. tract	Calf no. 99	360	365	371	Av.
	mg./gm. ingesta				
Rumen	2.85	1.21	1.68	1.39	1.78
Omasum[a]					
Abomasum	1.61	0.91	0.91	0.59	1.01
SI-1[b]	1.30	0.80	0.85	0.74	0.92
SI-2	0.94	0.71	0.84	0.53	0.76
SI-3	0.79	0.58	0.47	0.57	0.60
SI-4	0.56	0.42	0.44	0.56	0.50
SI-5	0.42	0.51	0.57	0.48	0.50
SI-6	0.51	0.63	0.70	0.38	0.56
Cecum	0.68	0.89	0.95	0.53	0.76
LI-1[c]	0.76	0.79	0.67	0.42	0.66
LI-2	0.58	0.40	0.59	0.44	0.50

[a]No ingesta in the omasum.

[b]SI = small intestine.

[c]LI = large intestine.

TABLE XXXIII

INTESTINAL CONCENTRATIONS OF POTASSIUM IN CALVES FED CONCENTRATE RATIONS

Section of G.I. tract	Calf no. 372	373	377	380	Av.
			mg./gm. ingesta		
Rumen	0.41	0.84	0.71	0.34	0.58
Omasum	0.59	0.67	0.52	0.48	0.57
Abomasum	0.31	0.34	0.36	0.31	0.33
SI-1[a]	0.68	0.64	1.06	0.91	0.82
SI-2	0.95	0.75	0.48	1.02	0.80
SI-3	0.51	0.63	0.36	0.62	0.54
SI-4	0.58	0.53	0.47	0.66	0.56
SI-5	0.65	0.56	0.56	0.85	0.66
SI-6	0.74	0.48	0.45	0.67	0.59
Cecum	0.56	0.85	0.73	0.75	0.72
LI-1[b]	0.57	0.69	0.65	0.84	0.69
LI-2	0.64	0.36	0.31	0.92	0.56

[a]SI = small intestine.

[b]LI = large intestine.

TABLE XXXIV

INTESTINAL CONCENTRATIONS OF POTASSIUM IN CALVES FED CONCENTRATE AND HAY RATIONS

Section of G. I. tract	Calf no. 291	362	370	Av.
		mg./gm. ingesta		
Rumen	1.14	0.83	0.56	0.84
Omasum	1.49	1.17	1.04	1.23
Abomasum	0.60	0.56	0.47	0.54
SI-1[a]	0.94	0.52	0.63	0.66
SI-2	0.91	0.41	1.01	0.78
SI-3	0.94	0.64	0.74	0.77
SI-4	0.94	0.54	0.67	0.72
SI-5	0.73	0.62	0.64	0.66
SI-6	0.72	0.58	0.61	0.64
Cecum	1.44	1.04	0.90	1.13
LI-1[b]	0.84	0.84	0.88	0.85
LI-2	0.42	0.45	0.88	0.58

[a]SI = small intestine.

[b]LI = large intestine.

TABLE XXXV

INTESTINAL CONCENTRATIONS OF NITROGEN IN CALVES FED SEMIPURIFIED RATIONS

Section of G.I. tract	Calf no. 99	360	365	371	Av.
			mg./gm. ingesta		
Rumen	5.20	3.17	6.63	3.78	4.70
Omasum[a]					
Abomasum	3.25	a	5.37	2.80	3.81
SI-1[b]	5.83	6.15	5.72	5.00	5.63
SI-2	4.76	5.60	5.44	2.80	4.65
SI-3	4.55	6.00	3.72	3.68	4.49
SI-4	3.29	2.90	3.98	a	2.54
SI-5	1.94	2.63	a	1.50	1.52
SI-6	1.90	3.05	3.49	1.71	2.54
Cecum	3.13	4.99	5.09	3.89	4.28
LI-1[c]	8.12	4.69	7.15	3.85	5.95
LI-2	9.73	4.09	8.53	8.63	7.75

[a]No determination.

[b]SI = small intestine.

[c]LI = large intestine.

TABLE XXXVI

INTESTINAL CONCENTRATIONS OF NITROGEN IN CALVES FED CONCENTRATE RATIONS

Section of G.I. tract	Calf no. 372	373	377	380	Av.
			mg./gm. ingesta		
Rumen	3.29	4.57	4.70	2.73	3.82
Omasum	10.10	11.15	11.55	7.72	10.13
Abomasum	2.30	4.70	4.93	3.53	3.87
SI-1[a]	8.58	8.90	b	b	8.74
SI-2	10.96	10.94	7.87	b	9.92
SI-3	5.55	5.13	6.60	5.75	5.76
SI-4	5.23	4.82	5.22	4.96	5.06
SI-5	4.31	3.42	1.95	4.66	3.59
SI-6	3.26	3.18	2.34	3.79	3.14
Cecum	4.16	4.74	4.19	3.97	4.27
LI-1[c]	5.26	5.30	5.09	4.14	4.95
LI-2	5.62	5.49	5.68	5.36	5.54

[a]SI = small intestine.

[b]No determination.

[c]LI = large intestine.

TABLE XXXVII

INTESTINAL CONCENTRATIONS OF NITROGEN IN CALVES FED CONCENTRATE AND HAY RATIONS

Section of G.I. tract	Calf no. 291	362	370	Av.
		mg./gm. ingesta		
Rumen	4.57	4.03	4.40	4.33
Omasum	7.65	9.41	8.96	8.67
Abomasum	4.67	4.37	2.94	3.99
SI-1[a]	[b]	8.75	7.61	8.18
SI-2	8.64	8.77	[b]	8.70
SI-3	7.11	5.21	5.43	5.92
SI-4	4.48	4.05	4.73	4.42
SI-5	2.68	3.02	2.49	2.73
SI-6	3.02	2.95	2.77	2.91
Cecum	4.47	3.39	3.78	3.88
LI-1[c]	4.75	4.03	3.09	3.96
LI-2	5.17	5.46	4.62	5.08

[a]SI = small intestine.

[b]No determination.

[c]LI = large intestine.

TABLE XXXVIII

INSORPTION OF Ca^{45} FROM ISOLATED JEJUNAL SEGMENTS OF CALVES

Consecutive 30 ml. blood samples	Calf no. 1[a]	2	3	4	5	6	7	8	Av.
	% dose/ml. blood/gm. ashed intestine X(10^{-3})								
1	4	15	1	37	69	13	30		20
2	7	35	3	51	70	25	11		29
3	13	41	5	67	66	39	19		36
4	18	61	7	96	92	57	18		50
5	37	65	7	94	85	64	21		53
6	49	62	8	77	115	49	40		57
7	35	78	14	101	164	46	44		69
8	33	90	19	95	49	42	51		54
9	62	70	17	102	122	34	56		66
10	20	64	16	54	75	35	47		44
11	22	78	15	[a]	86	32	65		50
12	19	73	13	[a]	99	31	69		51

[a]No blood samples obtained.

TABLE XXXIX

INSORPTION OF Sr^{89} FROM ISOLATED JEJUNAL SEGMENTS OF CALVES

Consecutive 30 ml. blood samples	Calf no. 1[a]	2	3	4	5	6	7	8	Av.
	% dose/ml. blood/gm. ashed intestine X(10^{-3})								
1		2	6	1	27	48	9	2	14
2		4	11	3	32	30	20	7	15
3		6	17	5	45	22	26	11	17
4		12	25	8	70	23	36	10	26
5		25	21	8	75	18	40	11	28
6		25	21	8	60	25	33	18	27
7		23	24	14	69	38	32	20	31
8		17	28	20	78	11	27	22	29
9		33	24	17	87	28	23	23	34
10		10	20	15	40	16	22	21	21
11		10	24	25	[a]	21	22	27	20
12		10	21	13	[a]	23	20	29	19

[a]No blood samples obtained.

TABLE XL

INSORPTION OF K^{42} AND Na^{24} FROM ISOLATED JEJUNAL SEGMENTS OF CALVES

Consecutive 30 ml. blood samples	Na^{24}			K^{42}				
	Calf no.			Calf no.				
	2	7	Av.	3	4	5	6	Av.
	% dose/ml. blood/gm. ashed intestine $X(10^{-3})$							
1	8	51	30	11	1	14	60	21
2	17	106	62	11	3	21	26	15
3	32	137	85	13	3	28	12	14
4	49	192	120	19	3	29	13	16
5	115	205	160	24	3	28	9	16
6	157	163	160	30	4	28	12	18
7	96	135	116	34	8	30	31	26
8	77	113	95	35	7	35	14	23
9	139	95	117	39	6	47	15	27
10	49	88	69	42	9	44	14	27
11	42	75	59	43	12	[a]	16	18
12	54	66	60	45	8	[a]	15	17

[a]No blood samples obtained.

TABLE XLI

INSORPTION OF Ca^{45} FROM ISOLATED ILEAL SEGMENTS OF CALVES

Consecutive 30 ml. blood samples	Calf no. 1	2	3	4	5	6	7	8	Av.
	% dose/ml. blood/gm. ashed intestine $X(10^{-5})$								
1	62	[a]	94	14	17	18	5	16	32
2	72	[a]	171	75	15	19	28	116	71
3	55	23	155	60	16	21	49	254	78
4	68	12	235	82	25	24	65	221	92
5	81	20	217	55	23	19	91	175	85
6	88	13	267	83	24	25	59	224	98
7	47	14	266	91	44	37	189	243	116
8	35	15	194	102	46	30	213	258	112
9	29	16	260	102	41	28	211	275	120
10	61	25	215	94	66	36	239	317	132
11	50	24	170	77	34	31	225	310	115
12	98	27	153	68	41	23	356	290	132

[a]Blood samples lost.

TABLE XLII

INSORPTION OF Sr^{89} FROM ISOLATED ILEAL SEGMENTS OF CALVES

Consecutive 30 ml. blood samples	Calf no. 1	2	3	4	5	6	7	8	Av.
	% dose/ml. blood/gm. ashed intestine $X(10^{-5})$								
1	43	a	80	28	16	15	4	11	28
2	24	a	138	68	12	23	24	68	51
3	35	18	137	57	16	21	40	154	67
4	42	11	152	69	20	25	51	147	65
5	46	17	166	41	17	16	87	108	62
6	49	10	213	68	16	29	53	141	72
7	23	11	224	72	26	24	170	164	89
8	20	12	167	93	29	18	179	162	85
9	16	13	207	78	22	24	187	179	91
10	35	19	186	75	29	26	215	201	98
11	29	20	151	57	13	24	229	192	89
12	54	19	115	56	11	16	317	188	97

[a]Blood samples lost.

TABLE XLIII

INSORPTION OF K^{42} AND Na^{24} FROM ISOLATED ILEAL SEGMENTS OF CALVES

Consecutive 30 ml. blood samples	Na^{24} Calf no. 1	2	7	Av.	K^{42} Calf no. 3	4	Av.
	% dose/ml. blood/gm. ashed intestine $X(10^{-4})$						
1	15	[a]	1	8	18	4	11
2	13	[a]	8	11	23	10	17
3	14	18	17	16	27	8	17
4	18	18	27	21	30	8	19
5	23	17	37	26	31	8	19
6	14	16	47	26	37	11	24
7	10	18	60	30	42	12	27
8	10	24	74	36	46	17	32
9	9	27	85	40	48	14	31
10	11	32	91	44	50	16	33
11	10	32	95	46	52	15	33
12	15	33	104	51	51	18	35

[a]Blood samples lost.

TABLE XLIV

RELATIVE INSORPTION OF Ca^{45} AND Sr^{89} FROM ADJACENT ISOLATED JEJUNAL SEGMENTS OF CALVES CONTAINING 5.0 mM. Ca, 2.5 mM. Ca AND 2.5 mM. Sr, AND 5.0 mM. Sr/l. IN THE LUMINAL SOLUTIONS[a]

Consecutive 25 ml. blood samples	Calf no. 13	14	15	16	Av.
		5.0 mM. Ca/l.			
1	0.84	0.99	0.84	0.75	0.85
2	0.91	0.90	1.08	0.73	0.91
3	0.91	0.60	1.17	0.73	0.85
4	0.95	0.52	1.22	0.70	0.85
5	0.94	0.43	1.20	0.72	0.82
6	0.93	0.44	1.16	0.73	0.82
7	0.93	0.44	1.26	0.70	0.83
8	0.92	0.53	1.49	0.69	0.91
		2.5 mM. Ca and 2.5 mM. Sr/l.			
1	1.64	1.46	1.07	1.12	1.32
2	1.66	2.43	1.53	0.84	1.62
3	1.43	1.66	1.49	0.86	1.36
4	1.80	2.06	1.68	0.91	1.61
5	1.62	1.86	1.52	0.92	1.48
6	1.63	1.74	1.54	0.97	1.47
7	1.66	1.66	1.62	1.06	1.50
8	1.64	2.07	1.64	1.08	1.61
		5.0 mM. Sr/l.			
1	2.16	2.58	b	0.95	1.90
2	2.31	2.44	b	1.07	1.94
3	3.40	2.24	b	1.11	2.25
4	2.34	2.78	b	1.18	2.10
5	2.65	2.25	b	1.15	2.02
6	2.36	2.27	b	1.17	1.93
7	1.88	2.43	b	1.18	1.83
8	2.16	2.38	b	1.10	1.88

[a]Expressed as % dose Sr^{89}/% dose Ca^{45}.

[b]No blood samples obtained.

TABLE XLV

INSORPTION OF Ca^{45} FROM ADJACENT ISOLATED JEJUNAL SEGMENTS OF CALVES CONTAINING 288, 383, AND 553 mOs. SOLUTIONS[a]

Consecutive 25 ml. blood samples	Calf no. 9	10	11	12	Av.
		288 mOs. solution			
1	18	10	28	7	16
2	57	34	37	33	40
3	84	41	41	60	57
4	92	38	53	87	68
5	101	34	63	105	76
6	114	34	63	108	80
7	106	41	64	114	81
8	112	41	73	138	91
		383 mOs. solution			
1	17	7	11	2	9
2	34	16	24	8	21
3	42	18	51	12	31
4	39	24	50	18	33
5	47	b	63	21	33
6	26	b	75	26	32
7	37	b	79	35	38
8	31	b	89	38	40
		553 mOs. solution			
1	4	1	7	2	4
2	9	2	13	7	8
3	13	3	19	11	12
4	18	4	43	18	21
5	18	5	46	22	23
6	19	6	51	22	25
7	19	6	68	28	30
8	18	7	94	26	36

[a]Expressed as % dose/ml. blood/gm. ashed intestine $X(10^{-3})$.

[b]No blood samples obtained.

TABLE XLVI

INSORPTION OF Sr^{89} FROM ADJACENT ISOLATED JEJUNAL SEGMENTS OF CALVES CONTAINING 288, 383, AND 553 mOs. SOLUTIONS[a]

Consecutive 25 ml. blood samples	Calf no. 9	10	11	12	Av.
		288 mOs. solution			
1	15	5	22	8	13
2	45	15	31	27	30
3	71	18	35	51	44
4	80	17	45	72	54
5	86	15	53	88	61
6	93	16	48	89	62
7	90	19	51	91	63
8	92	19	57	105	68
		383 mOs. solution			
1	7	4	9	2	6
2	17	8	18	6	12
3	26	9	39	11	21
4	19	13	38	16	22
5	32	b	49	20	34
6	15	b	61	22	33
7	21	b	62	29	37
8	14	b	70	30	38
		553 mOs. solution			
1	3	1	5	4	3
2	5	1	10	13	7
3	9	2	14	22	12
4	15	2	33	32	21
5	10	3	38	37	22
6	10	3	38	41	23
7	10	3	58	50	30
8	9	5	75	47	34

[a]Expressed as % dose/ml. blood/gm. ashed intestine $X(10^{-3})$.

[b]No blood samples obtained.

TABLE XLVII

EFFECTS OF ALTERING LUMINAL SOLUTIONS (ISOTONIC → HYPERTONIC) IN THE SAME ISOLATED JEJUNAL SEGMENTS OF CALVES UPON Ca^{45} AND Sr^{89} INSORPTION[a]

Consecutive 15 ml. blood samples	Ca^{45} Calf no. 19	21	24	Av.	Sr^{89} Calf no. 19	21	24	Av.
	Isotonic (290 mOs.) luminal solution							
1	5	3	2	3	3	3	2	3
2	9	15	1	8	5	12	2	6
3	8	22	2	11	7	18	3	9
4	11	27	3	14	7	21	3	10
5	16	29	3	16	10	22	2	11
6	21	34	8	21	13	26	4	14
7	27	30	13	23	15	26	6	16
8	35	40	17	31	19	31	7	19
9	36	32	21	30	20	24	7	17
10	32	34	17	28	19	26	6	17
11	51	33	21	35	29	27	7	21
12	54	31	24	36	29	24	9	21
13	68	40	26	45	36	32	9	26
14	64	49	35	49	34	35	12	27
15	82	42	30	51	45	31	11	29
16	83	29	34	49	45	21	11	26
	Hypertonic (396 mOs.) luminal solution							
17	52	19	22	31	46	14	23	28
18	54	21	20	32	42	17	20	26
19	51	19	8	26	46	14	7	22
20	50	13	15	26	47	11	10	23
21	39	13	11	21	30	9	5	15
22	47	13	15	25	59	9	8	25
23	48	13	3	21	39	10	12	20
24	44	15	10	23	37	11	5	18
25	54	9	30	31	53	9	28	30
26	51	16	21	29	47	15	18	27
27	45	25	32	34	41	23	14	26
28	49	12	13	25	46	12	9	22
29	48	11	15	25	51	11	17	26
30	53	30	11	31	61	29	6	32
31	49	33	3	28	68	31	1	33
32	48	36	4	29	76	36	2	38

TABLE XLVII (continued)

Consecutive 15 ml. blood samples	Ca^{45} Calf no. 19	21	24	Av.	Sr^{89} Calf no. 19	21	24	Av.
				4×10^{-3} M. iodoacetate				
33	43	14	6	21	55	11	4	27
34	43	33	11	29	54	29	6	33
35	40	21	13	25	63	20	10	31
36	36	23	9	23	56	21	10	29
37	30	15	9	18	45	10	12	22
38	34	22	9	18	43	22	10	25
39	32	20	17	23	40	18	13	24
40	28	9	3	13	32	11	2	15
41	27	19	2	16	30	15	2	16
42	24	7	3	11	28	6	2	12
43	26	7	3	12	29	5	3	12
44	22	11	8	14	24	8	10	14
45	20	11	5	12	21	8	6	12
46	15	5	23	14	20	3	8	10
47	18	7	22	16	18	5	8	10
48	11	5	14	10	15	3	10	9

[a]Expressed as % dose/ml. plasma $X(10^{-3})$.

TABLE XLVIII

EFFECTS OF ALTERING LUMINAL SOLUTIONS (HYPERTONIC ⟶ ISOTONIC) IN THE SAME ISOLATED JEJUNAL SEGMENTS OF CALVES UPON Ca^{45} AND Sr^{89} INSORPTION[a]

Consecutive 15 ml. blood samples	Ca^{45} Calf no.					Sr^{89} Calf no.				
	17	20	22	23	Av.	17	20	22	23	Av.
Hypertonic (396 mOs.) luminal solution										
1	2	-	1	3	2	2	2	1	3	2
2	8	3	4	6	5	6	4	3	5	5
3	15	8	16	13	13	10	7	8	10	9
4	21	22	36	14	23	14	19	17	8	15
5	15	30	88	15	37	19	27	42	9	24
6	23	45	87	13	42	22	33	43	9	27
7	43	38	114	14	52	15	35	60	9	30
8	30	48	111	13	51	22	26	56	10	29
9	34	76	125	19	64	24	60	70	15	42
10	36	55	101	24	54	27	86	53	13	45
11	41	65	93	28	57	31	57	51	16	39
12	39	58	105	18	54	30	45	44	9	32
13	50	50	81	28	52	40	41	50	13	36
14	46	54	103	26	57	39	61	57	13	43
15	59	72	99	28	64	47	59	56	14	44
16	56	70	81	26	58	50	50	47	11	40
Isotonic (290 mOs.) luminal solution										
17	47	115	67	12	60	39	77	40	5	40
18	111	75	98	18	75	62	44	74	8	47
19	81	75	146	37	85	67	57	122	13	65
20	78	77	160	41	89	71	67	132	17	69
21	82	91	164	33	92	75	47	138	14	66
22	89	74	173	61	99	79	56	140	25	75
23	90	76	172	68	102	75	42	143	29	72
24	84	85	160	99	107	73	46	132	34	71
25	70	83	156	115	106	59	62	131	42	74
26	90	88	178	115	118	71	57	138	56	81
27	88	87	176	179	133	73	60	136	106	94
28	94	71	180	181	132	76	61	140	108	96
29	101	74	182	188	136	79	67	139	110	99
30	105	80	182	186	138	79	80	137	109	101
31	104	86	181	185	139	84	67	141	109	100
32	102	89	184	187	141	90	90	142	110	108

TABLE XLVIII (continued)

Consecutive 15 ml. blood samples	Ca^{45} Calf no.					Sr^{89} Calf no.				
	17	20	22	23	Av.	17	20	22	23	Av.
				4×10^{-3} M. iodoacetate						
33	114	160	180	b	151	93	136	140	b	130
34	129	46	176	b	150	110	59	138	b	106
35	113	50	162	b	108	94	47	126	b	89
36	91	41	148	b	93	72	36	120	b	76
37	76	13	239	b	73	60	15	105	b	60
38	54	42	110	b	69	41	46	89	b	59
39	51	35	91	b	59	42	29	73	b	48
40	45	48	83	b	59	33	35	68	b	45
41	41	44	74	b	53	31	38	60	b	43
42	34	50	62	b	49	26	36	48	b	37
43	31	55	49	b	45	22	43	40	b	35
44	24	57	41	b	41	16	49	34	b	33
45	18	51	30	b	33	12	40	24	b	25
46	17	37	25	b	26	10	31	21	b	21
47	14	35	20	b	23	9	31	19	b	20
48	12	21	18	b	17	7	17	18	b	14

[a]Expressed as % dose/ml. plasma $X(10^{-3})$.

[b]No blood samples obtained.

TABLE XLIX

EFFECTS OF ALTERING LUMINAL SOLUTIONS (2.5 mM. Ca AND 2.5 mM. Sr ⟶ 5.0 mM. Ca) IN THE SAME ISOLATED JEJUNAL SEGMENTS OF CALVES UPON Ca^{45} AND Sr^{89} INSORPTION[a]

Consecutive 15 ml. blood samples	Ca^{45} Calf no. 18	19	21	24	Av.	Sr^{89} Calf no. 18	19	21	24	Av.
	2.5 mM. Ca and 2.5 mM. Sr luminal solution									
1	2	2	1	-	1	2	1	1	2	2
2	7	8	3	8	7	8	5	2	5	5
3	13	14	4	16	12	13	9	3	9	9
4	15	21	7	19	16	15	15	5	11	12
5	19	26	9	23	19	20	21	7	15	16
6	26	34	14	20	24	27	27	11	13	20
7	33	82	15	27	39	34	78	10	16	35
8	35	63	17	31	37	36	70	13	21	35
9	37	44	16	31	32	38	38	13	20	27
10	39	47	22	40	37	45	46	20	24	34
11	41	47	22	43	38	46	39	19	27	33
12	35	48	24	39	37	47	48	21	28	36
13	50	52	24	44	43	54	51	20	30	39
14	49	54	26	51	45	56	51	22	31	40
15	49	51	26	51	44	55	52	22	33	41
16	47	44	32	51	44	54	46	28	32	40
	5.0 mM. Ca luminal solution									
17	81	59	12	28	45	91	54	8	17	43
18	88	52	14	31	46	97	52	9	18	44
19	89	56	11	31	47	101	55	8	20	46
20	80	b	7	35	41	91	b	5	20	39
21	78	b	23	35	45	88	b	16	22	42
22	69	b	35	37	47	80	b	27	19	42
23	69	b	34	33	45	76	b	26	19	40
24	58	b	37	38	44	91	b	30	21	47
25	67	b	39	41	49	71	b	34	25	43
26	68	b	47	47	54	73	b	39	26	46
27	66	b	25	47	46	74	b	22	28	41
28	66	b	36	46	49	71	b	32	28	43
29	66	b	44	52	54	72	b	42	32	49
30	53	b	55	59	56	82	b	53	38	58
31	77	b	50	60	62	84	b	50	38	57
32	81	b	63	59	68	91	b	57	37	62

TABLE XLIX (continued)

Consecutive 15 ml. blood samples	Ca^{45} Calf no. 18	19	21	24	Av.	Sr^{89} Calf no. 18	19	21	24	Av.
				4×10^{-3} M. iodoacetate						
33	90	b	58	68	72	105	b	59	47	70
34	81	b	63	53	66	95	b	65	36	65
35	77	b	65	70	71	83	b	65	47	65
36	64	b	34	59	52	71	b	31	35	46
37	59	b	42	57	53	64	b	41	34	45
38	53	b	39	57	50	60	b	40	36	45
39	48	b	22	62	44	55	b	24	35	38
40	52	b	26	61	46	51	b	27	40	39
41	46	b	22	55	41	53	b	22	31	35
42	45	b	23	55	41	49	b	21	36	35
43	49	b	21	47	39	49	b	21	33	34
44	41	b	23	b	32	47	b	22	b	34
45	49	b	14	b	32	48	b	13	b	30
46	37	b	24	b	30	41	b	22	b	31
47	46	b	17	b	31	52	b	14	b	33
48	53	b	9	b	31	56	b	9	b	32

[a]Expressed as % dose/ml. plasma $X(10^{-3})$.

[b]No blood samples obtained.

TABLE L

EFFECTS OF ALTERING LUMINAL SOLUTIONS (5.0 mM. Ca ⟶ 2.5 mM. Ca AND 2.5 mM. Sr) IN THE SAME ISOLATED JEJUNAL SEGMENTS OF CALVES UPON Ca^{45} AND Sr^{89} INSORPTION[a]

Consecutive 15 ml. blood samples	Ca^{45} Calf no. 17	20	22	23	Av.	Sr^{89} Calf no. 17	20	22	23	Av.
	5.0 mM. Ca luminal solution									
1	12	1	10	9	8	6	1	5	7	5
2	21	2	9	23	14	14	2	7	14	9
3	26	7	15	45	23	24	6	10	21	15
4	32	8	18	64	31	25	8	14	33	20
5	38	32	19	77	41	30	27	14	37	27
6	41	18	22	51	33	30	16	12	24	21
7	35	29	24	52	35	30	27	14	25	24
8	35	34	13	47	32	20	31	8	23	21
9	27	19	18	40	35	14	20	11	18	18
10	82	49	30	56	54	57	52	17	23	38
11	88	53	28	61	58	62	46	16	28	38
12	79	57	30	80	62	60	51	17	37	41
13	94	63	33	58	62	77	52	18	27	44
14	84	67	55	60	67	71	69	31	28	50
15	76	56	51	66	62	64	60	34	32	48
16	65	61	46	92	66	62	57	29	48	49
	2.5 mM. Ca and 2.5 mM. Sr luminal solution									
17	66	56	39	80	60	51	50	25	50	44
18	59	51	33	76	55	44	49	25	48	41
19	54	48	39	75	54	41	46	29	49	41
20	57	48	39	76	55	42	43	31	50	42
21	56	52	36	76	55	38	46	30	51	41
22	48	64	38	78	57	35	63	26	54	45
23	62	56	72	81	68	42	52	64	58	54
24	51	b	55	80	62	36	b	49	60	48
25	62	b	64	85	70	44	b	56	62	54
26	76	b	62	78	72	52	b	60	68	60
27	116	b	68	80	88	98	b	66	70	78
28	109	b	71	82	87	82	b	70	73	75
29	82	b	74	84	80	82	b	71	74	76
30	65	b	67	88	73	64	b	68	77	70
31	68	b	66	90	75	62	b	67	69	66
32	70	b	65	85	73	68	b	70	73	70

TABLE L (continued)

Consecutive 15 ml. blood samples	Ca^{45} Calf no. 17	20	22	23	Av.	Sr^{89} Calf no. 17	20	22	23	Av.
				4×10^{-3} M. iodoacetate						
33	72	b	80	91	81	52	b	62	70	61
34	64	b	77	83	75	45	b	62	67	58
35	38	b	71	81	63	30	b	64	68	54
36	21	b	74	72	56	17	b	70	71	53
37	16	b	63	61	47	14	b	64	66	48
38	14	b	61	56	43	13	b	64	60	46
39	14	b	53	58	42	11	b	60	55	42
40	11	b	47	43	34	10	b	58	51	40
41	10	b	48	51	36	9	b	51	47	49
42	14	b	32	29	25	12	b	44	41	43
43	b	b	35	39	37	b	b	38	40	39
44	b	b	30	34	32	b	b	39	35	37
45	b	b	28	20	24	b	b	34	31	33
46	b	b	25	28	27	b	b	36	30	33
47	b	b	29	21	25	b	b	40	32	36
48	b	b	34	15	20	b	b	36	23	30

[a]Expressed as % dose/ml. plasma $X(10^{-3})$.

[b]No blood samples obtained.

TABLE LI

INSORPTION OF Ca^{45} AND Sr^{89} FROM ISOLATED JEJUNAL SEGMENTS OF CALVES CONTAINING 5.0 mM. Ca/l.

Consecutive 5 ml. blood samples	Ca^{45} Calf no. 27	28	31	Av.	Sr^{89} Calf no. 27	28	31	Av.
	% dose/ml. plasma/gm. dry intestine X(10^{-3})							
1	1	3	3	2	19	5	12	12
2	9	6	8	8	18	16	19	18
3	12	15	14	14	15	15	20	17
4	23	22	27	24	15	15	24	18
5	27	27	30	28	27	19	26	24
6	30	30	31	30	24	26	21	24
7	31	30	31	31	30	24	22	25
8	48	36	33	39	29	25	24	26
9	47	40	48	45	29	29	36	31
10	49	42	40	43	32	30	32	31
11	39	43	46	43	45	30	33	36
12	46	48	49	44	33	41	38	37
13	52	47	54	51	45	32	44	40
14	57	50	55	54	29	35	48	37
15	56	52	51	53	40	32	48	40
16	51	53	55	53	42	30	51	41
17	55	35	57	56	44	34	41	40
18	50	60	66	60	39	35	54	43
19	66	59	54	59	60	38	47	48
20	57	61	53	57	45	34	42	40
21[a]	54	62	60	59	38	35	46	40
22	54	51	51	52	39	36	41	39
23	47	42	49	46	30	39	40	36
24	42	38	39	40	36	33	38	36
25	39	37	28	35	27	37	36	33
26	37	35	24	32	28	33	36	32
27	39	35	24	33	39	32	34	35
28	36	34	23	31	33	36	35	35

[a]Iodoacetate injection.

TABLE LII

INSROPTION OF Ca^{45} AND Sr^{89} FROM ISOLATED JEJUNAL SEGMENTS OF CALVES CONTAINING 10.0 mM. Ca/l.

Consecutive 5 ml. blood samples	Ca^{45} Calf no. 27	28	32	Av.	Sr^{89} Calf no. 27	28	32	Av.
	% dose/ml. plasma/gm. dry intestine X(10^{-3})							
1	2	1	3	2	6	14	11	10
2	8	9	12	10	20	25	16	20
3	19	32	23	25	26	44	31	34
4	25	26	24	25	27	28	15	23
5	19	24	25	23	32	29	15	25
6	25	27	27	26	32	29	15	25
7	24	26	27	26	31	28	24	28
8	27	28	29	28	32	28	23	28
9	30	30	30	30	32	29	24	28
10	30	34	30	31	33	28	23	28
11	33	32	30	32	34	24	23	27
12	36	33	30	33	33	43	37	38
13	41	38	43	41	39	57	34	43
14	47	39	32	39	30	54	36	40
15	47	40	36	41	35	55	35	42
16	42	47	33	41	35	57	31	41
17	51	52	39	47	42	55	37	45
18	113	49	35	66	54	55	31	47
19	54	58	34	49	44	48	27	40
20	56	52	38	49	46	45	25	39
21[a]	43	39	45	42	52	47	23	41
22	37	35	38	37	42	42	23	36
23	27	29	32	26	30	36	23	30
24	28	25	31	28	34	39	24	32
25	27	28	27	27	32	35	21	29
26	20	25	28	24	41	37	29	36
27	24	26	27	26	31	32	21	28
28	21	25	26	23	34	33	18	28

[a]Iodoacetate injection.

TABLE LIII

INSORPTION OF Ca^{45} AND Sr^{89} FROM ISOLATED JEJUNAL SEGMENTS OF CALVES CONTAINING 1.0 mM. Sr/l.

Consecutive 5 ml. blood samples	Ca^{45} Calf no. 29	30	31	Av.	Sr^{89} Calf no. 29	30	31	Av.
	% dose/ml. plasma/gm. dry intestine X(10^{-3})							
1	1	3	4	3	36	20	31	29
2	6	8	9	8	38	30	36	35
3	35	23	31	30	46	30	41	39
4	[a]	30	36	33	[a]	35	38	37
5	63	40	51	51	53	40	43	45
6	83	49	63	65	69	47	59	58
7	101	61	64	75	60	54	57	57
8	88	55	68	70	62	62	65	63
9	86	57	59	67	63	65	71	66
10	91	61	73	75	63	72	78	71
11	80	64	74	73	58	69	73	67
12	81	65	84	77	66	73	58	66
13	94	71	87	84	85	59	71	72
14	74	71	83	76	65	81	75	74
15	112	61	89	87	77	66	82	75
16	98	78	73	83	68	107	68	81
17	87	67	84	79	71	124	78	91
18	96	65	88	83	73	142	79	98
19	89	78	92	86	66	160	88	105
20	107	63	89	86	69	221	85	125
21[b]	111	80	93	95	83	226	74	128
22	73	57	77	69	75	122	77	91
23	51	45	68	55	73	124	62	86
24	43	40	54	46	70	130	64	88
25	33	34	41	36	65	110	69	81
26	22	27	38	29	67	109	71	82
27	18	26	34	36	71	105	66	81
28	14	22	29	22	80	101	63	81

[a]Blood sample lost.

[b]Iodoacetate injection.

TABLE LIV

INSORPTION OF Ca^{45} AND Sr^{89} FROM ISOLATED JEJUNAL SEGMENTS OF CALVES CONTAINING 5.0 mM. Sr/l.

Consecutive 5 ml. blood samples	Ca^{45} Calf no. 29	31	32	Av.	Sr^{89} Calf no. 29	31	32	Av.
	% dose/ml. plasma/gm. dry intestine X(10^{-3})							
1	5	2	4	4	30	18	19	22
2	11	4	13	9	33	23	23	26
3	33	18	20	24	37	30	28	32
4	37	22	22	27	44	29	32	35
5	46	25	27	33	39	37	33	36
6	54	27	32	38	38	33	31	34
7	69	31	28	43	48	37	32	39
8	71	40	41	51	39	39	34	37
9	86	36	42	55	45	48	42	45
10	76	45	51	57	48	53	46	49
11	96	52	62	70	54	53	49	52
12	94	54	57	68	62	59	56	59
13	87	62	59	69	51	66	54	57
14	99	64	76	80	51	65	53	56
15	114	60	82	85	57	55	51	54
16	123	60	86	90	55	47	46	49
17	130	55	89	91	57	45	46	49
18	100	61	75	79	54	48	46	49
19	97	62	74	78	63	54	54	57
20	102	60	71	78	52	57	50	53
21[a]	96	56	58	70	51	57	49	52
22	65	45	40	50	54	51	48	51
23	74	46	45	53	52	48	45	48
24	66	40	40	49	60	55	53	56
25	65	35	38	46	52	42	42	45
26	56	27	33	39	55	41	65	54
27	57	30	34	40	49	41	40	43
28	59	23	34	39	51	35	38	41

[a]Iodoacetate injection.