THE UNIVERSITY OF MANITOBA

INFLUENCE OF RYE (*Secale cereale* L.) GRAIN ON THE WATER AND ELECTROLYTE METABOLISM OF ADULT ROOSTERS AND ON THE SALT REQUIREMENT OF GROWING CHICKENS

by

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ABSTRACT

A preliminary study with 10 colostomized adult roosters (SCWL) was conducted to test a hypothesis that there is a difference in water and/or electrolyte metabolism between rye-fed birds and corn-fed controls. A water-extracted rye diet was included in the experimental design to determine the influence of the water extraction process on water metabolism of the chicken. The level of dietary salt was 0.4% in all diets.

Data of water intake, urine volume and osmolality led to the conclusion that a severe diuresis had developed in birds fed the rye diet. Data also indicated that a mild diuresis may have developed in some of the birds fed the water-extracted rye diet.

An in depth study of water and electrolyte metabolism was carried out with 24 adult roosters (SCWL) fed either a corn or rye diet supplemented with high (1.0%) and low (0.4%) levels of salt. A water-extracted rye diet and a corn diet containing 12% freeze-dried water extract of rye (rye extract), both supplemented with 1.0% salt, were used to determine the effect of the water extraction process of rye on water and electrolyte metabolism in the chicken. A colostomy operation was performed on each bird to facilitate the separate collection of urine and feces. Data were collected before and after the operation to allow for a detailed interpretation of the effects of experimental diets on water and electrolyte metabolism.

Intact roosters fed rye diets were more resistant to an excessive intake of salt than were birds fed corn diets. When colostomized, rye-fed birds were more susceptible to salt deficiency, especially sodium, than were birds fed corn diets. The colostomized birds fed the water-extracted rye diet containing 1.0% salt displayed similar sodium deficiency symptoms, i.e., diuresis, to those observed with rye-fed birds. It was concluded, therefore, that rye contains substance(s) which decreases sodium absorption in the gut. The water extraction process did not completely eliminate the substance(s) from rye, indicating that most of the substance(s) are water-insoluble.

Data of dry matter metabolizability of experimental diets and bulk density (g/mℓ) of dried feces indicated that rye is high in dietary fiber which is hardly influenced by the water extraction process. Data of ionic concentrations of dried feces indicated that the dietary fiber present in rye does not function as a weak monocation exchange resin in the gut, making sodium ions unavailable to the body. Alternatively it is suggested that the dietary fiber present in digesta of the lower gut functions as a diluting agent, exerting an effect of a physical barrier to the movement of sodium ions toward intestinal mucosa. The fact that the major route of sodium excretion in rye-fed birds was via feces while urine was the major excretory pathway of sodium in corn-fed birds adds credence to this view.

The substance(s) which cause the sticky excreta condition among rye-fed birds was found to be water-soluble. When added to a corn diet at a level of 12%, however, the rye extract did not increase the viscosity of excreta and/or feces among adult roosters. Experimental evidence also

indicates that the rye extract reduces the sodium ion absorption in the gut. The mechanism(s) by which the rye extract causes this phenomenon, however, is not well understood.

The colostomy operation appeared to force the birds to drink more water. In addition, colostomized birds required more salt to maintain homeostasis indicating that the colon, not the cloaca, plays an important role in the post-renal modification of urine for normal economy of water and salt in intact birds.

A series of feeding trials were conducted to determine the influence of graded levels of dietary salt supplementation on the growth performance of young broilers and cockerels. Growth rate and feed conversion efficiency in young chickens fed rye diets improved significantly when the dietary salt level increased from 0.3% to 0.6%, but not to a level equivalent to that of corn-fed birds. The relative growth rate of chickens fed rye diets supplemented with 0.3% salt was 78-86% of that of birds fed rye diets containing 0.6% dietary salt.

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The author wishes to dedicate this thesis to his wife and parents.

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GENERAL INTRODUCTION

Rye (*Secale cereale* L.) can be grown in areas that are generally not suitable for growing other cereal grains because of its extreme hardiness and ability to grow in soils of low fertility. Greatest production is in the cool temperate zones of the world, but it can also grow in the semi-arid regions near deserts and at high altitudes. It enjoys the widest distribution of all the cereal crops. Although the crop rye has tremendous agronomic potential, there has not been much incentive to produce the crop because of limited market possibilities. An obvious major outlet for rye is as a livestock and poultry feed but certain problems associated with the feeding of rye must be overcome before the full potential of this market can be realized.

One of the problems associated with feeding rye to poultry is that birds on rye-based diets excrete very sticky and/or watery droppings, an unfavorable condition in any management system. Many investigators have reported "sticky" or "watery" droppings among chickens fed diets based on barley (Willingham *et al*., 1959) and rye (North, 1933; Halpin *et al*., 1936a). It was also noted that water consumption by the birds was linearly correlated with the moisture content of the excreta. This observation indicates that the water turn-over rate in birds excreting sticky and/or watery droppings is faster than that in normal birds. When the moisture content of excreta increases, it should be due to either the increased flow of urine or the increased fecal water excretion, or both. Because of the common excretory pathway (cloaca) for urine and feces, separate collection of urine and feces is particularly difficult in the fowl. In order to confront the sticky and/or watery dropping problem, however, the separate collection of feces and urine is necessary. Since the water metabolism is greatly influenced by salt metabolism, a thorough study of water and electrolyte metabolism in birds excreting sticky and/or watery droppings is required to understand the source and cause of the increased excreta moisture.

The present experiments were initiated under a hypothesis that water and electrolyte metabolism in rye-fed birds is quite different from that of corn-fed birds, because the latter do not excrete wet droppings. The separation and collection of feces and urine in this study was achieved by the exteriorization of the colon (colostomy).

LITERATURE REVIEW

I. Nutritive Value of Rye for Poultry

A. Introduction

The use of rye in poultry diets has been extremely limited, because it causes several unfavorable phenomena when fed to poultry. Most of the literature dealing with the nutritive value of rye indicate that it is inferior to corn or wheat in its feeding value for poultry. During the past decades many attempts have been made to improve the feeding value of rye. Among them are several physicochemical treatments including water treatment and pelleting. In addition, feed additives, i.e., enzymes and antibiotics, have been incorporated in the diet to improve the feeding value of rye. Some of the attempts were partially successful, but as yet much of the problem still remains to be resolved.

B. Inferior nutritional quality of rye for poultry

An early study (Halpin _et_ _al_., 1936a) showed that the palatability of rye for pullets was the lowest among several grains tested. In two production trials with laying hens, however, these same authors found that including rye up to 45% of the diet had no adverse effect on rate of egg production. Results of a study by North (1933) indicated that rye could be used as a replacement for corn or barley up to 20% of the diet without affecting the rate of egg production although egg quality was decreased. In a recent study where rye was used at a level of 80% of the diet of laying hens, a sharp decline in egg production was observed (Fernandez _et_ _al_., 1973a). In short, it appears that rye should be used at moderate levels in the diets of laying hens.

Several workers have reported poor performance of broiler chickens fed diets containing rye. Smith and MacIntyre (1960) found that all-mash broiler diets containing rye resulted in poorer growth and feed efficiency than did similar diets containing wheat. A growth depression in broiler chickens fed diets containing 30% rye was also reported by Wilson and McNab (1975). Moran et al. (1970) ascertained that rye could comprise up to 25% of the grain component of a broiler diet without adverse effects on productive performance relative to controls even though litter moisture was significantly increased among rye-fed birds. Increases, however, in the percentage of rye to more than 25% of the grain fraction resulted in progressively poorer live performance, dressed yield and carcass quality. The data indicate that rye, per se, should not be fed to broiler chickens at levels in excess of 25%. In conclusion, rye has not been considered favorably as a poultry feed because of its poor nutritive qualities relative to other cereal grains. To use rye as a poultry feed to advantage, therefore, continued efforts are needed in research to discover methods of improving its nutritive value for poultry.

C. Nutritional improvements of rye by various physicochemical treatments

During the past decades numerous studies have been conducted to improve the nutritive value of rye and barley by physicochemical treatments. These treatments involve water soaking, cooking, water extraction, pelleting, autoclaving and acid and/or alkali treatments. Some of the treatments tested were found to be effective and others not. Even though some treatments proved to be effective, their effectiveness was usually not as great as expected.

Smith and MacIntyre (1960) found that pelleting improved the feeding value of rye for the chicken equivalent to that of wheat fed as an all-mash diet. Misir and Marquardt (1978a) showed an improved growth performance in chickens by pelleting rye diets, but this response was not consistent with the result of a later study (Misir and Marquardt, 1978b) which showed no effect of pelleting. More investigations need to be carried out with regard to the effectiveness of pelleting rye diets for poultry as a means of improving the nutritive value of rye.

It has long been recognized that the nutritive value of certain cereals, especially barley, can be improved by water treatment (Fry _et_ _al_., 1957). These workers prepared water-treated barley by soaking coarsely ground barley in water for 8 hours at room temperature, using one part grain to one part tap water (40^oC) by weight. After soaking, the grain was spread evenly and dried in a forced draft oven at 70^oC for 15-20 hours. In a subsequent study, Fry _et_ _al_. (1958) also reported that treatment of rye and wheat with water improved the nutritional value of these grains, but not to the same extent as for barley. In order to explain the effectiveness of water treatment of barley in improving its feeding value, Thomas _et_ _al_. (1960) carried out an extensive microbial study and demonstrated that microbial fermentation played a part in the improvement of barley by water treatment. In later studies, several antibiotics were incorporated into a mixture of barley and water (Thomas _et_ _al_., 1961a, 1961b). These antibiotics effectively prevented the improvement in nutritive quality expected as a result of water treatment. The reduction of the effect of water treatment by the incorporation of antibiotics was believed to be due to decreased microbial production of an enzyme(s) or other factor(s) which act on the barley substrate.

Willingham et al. (1960) reported that water treatment of barley was more effective than dietary enzyme supplements for improving the nutritive value of this grain. It was hypothesized that the water-treatment response was due to a combination of two effects, antibiotic synthesis and enzyme action. With regard to the former, the water-treated barley was shown to contain about 33 ppm of bacitracin-like activity. The fact that the enzyme β-glucanase was isolated from Bacillus subtilis which is known to be a common inhabitant of wheat flour (Rickes et al., 1962) may explain the latter response. It is highly probable that microorganisms such as Bacillus subtilis grow in the barley during the water treatment procedure producing enzymes which could act on the barley substrate during drying or later in the intestine following ingestion by birds.

Fernandez et al. (1973b) extracted rye with water to fractionate growth depressing factor(s) believed to be present in rye. Chickens receiving diets containing water extracted rye grew significantly better than did chickens fed diets containing unextracted rye. The dried water-extract of rye caused poor growth and a sticky excreta condition when added to a diet containing corn. Similar observations were also made by Misir and Marquardt (1978b) and Antoniou (1980). It appears that a factor(s) can be extracted from rye with water, which is associated with sticky excreta and poor growth when fed to growing chickens.

The irradiation of food or feedstuffs has frequently been shown to affect their nutritional value, and most studies have been directed to observe any possible harmful effect of irradiation. However, Moran et al. (1968) demonstrated some beneficial effects of cobalt-60 gamma irradiation on the utilization of wheat bran by the chicken. According to MacAuliffe _et al_. (1979) the factor present in rye that interferes with vitamin D utilization was largely inactivated by exposing the grain to 10 Mrad gamma rays. Also gamma irradiation of rye improved chicken growth and almost eliminated any growth depressing properties (Patel _et al_., 1980). Gamma irradiation of rye, therefore, seems to be more beneficial than harmful as far as nutrition of the chicken is concerned.

As reviewed above, many attempts have been made, with varying degrees of success, to improve the feeding value of low-quality cereal grains using various physicochemical treatments. However, the information obtained has been fragmentary and inconclusive. More research is needed in order to establish the type of changes brought about at the molecular level in a cereal grain by an effective treatment.

D. The effect of feed additives on the feeding value of rye

Since Moore _et al_. (1946) reported that streptomycin stimulated the growth of chickens, many researchers have conducted experiments to investigate the effect of dietary antibiotics on the performance of livestock and poultry. In addition, a great number of digestive enzymes have been produced commercially for the purpose of aiding the digestion in the gut. A brief review on the effect of dietary antibiotics and enzymes in relation to the nutritive value of some dietary constituents for poultry will be presented to aid in overall understanding of the problems associated with the feeding of rye to poultry.

An experiment with growing chickens was conducted to determine the M.E. of barley with added enzyme, and of water-treated barley (Potter et al., 1965). The M.E. value of western-grown barley (2.588 kcal/g) was increased to 3.059 kcal/g by the addition of a fungal enzyme and to 3.153 kcal/g by water treatment. The increase in M.E. of the barley caused either by the presence of the fungal enzyme in the diet or by water treatment was attributed to a significant increase in digestibility of protein and fat, and to a probable increase in digestibility of the N.F.E. fraction. However, it was not clear from this data as to why the digestibilities of protein, fat and N.F.E. fractions were improved.

The addition of enzymes and antibiotics to diets containing barley was found to improve growth rate of turkey poults (Moran and McGinnis, 1965). To explain these observations, it was hypothesized that the β-glucan fraction of barley supported the establishment of "undesirable" microflora which in turn proved detrimental to both poult growth and efficiency of feed utilization. The effects of the "undesirable" microflora might be modified either directly by the use of antibiotics or indirectly through the elimination of β-glucan by either enzyme (β-glucanase) addition or water treatment as discussed above. In a subsequent study, Moran and McGinnis (1968) found that the majority of antibiotics tested were either "effective" or "ineffective" in eliciting a growth response with both corn and barley grains; however, a few antibiotics prompted significantly better growth with one grain than with the other. This asymmetry of antibiotic action was explained in terms of an "altered" intestinal microflora due primarily to a specific dietary grain. Goatcher and McGinnis (1972) also observed that the growth response of chickens to different antibiotics was markedly influenced by the inclusion of ingredients such as rye, dry field beans, and other legume seeds in the diet. It may be concluded from the experimental data reviewed above that significant interrelationships exist between grain type and enzymes and/or antibiotics with regard to the influence of these feed additives on the nutritive value of grains.

There are some indications that the low nutritive value of rye is somehow related to the intestinal microflora. Wagner and Thomas (1978) examined the influence of diets containing rye or pectin on the intestinal flora of the young chicken. Ileum anaerobic counts of chickens fed diets containing rye or pectin were two or three logarithmic cycles greater than those of chickens fed a corn diet. The counts were not altered by dietary penicillin supplementation. However, the addition of penicillin to the diets always resulted in a large reduction in butyric acid and gas production as well as a decrease in spore-former counts by about 5 logarithmic cycles. It was suggested that a penicillin-sensitive spore-forming organism, that produces large amounts of gas and butyric acid fermentatively, may depress the growth of chickens fed rye or pectin. There was a strong indication that the organism might belong to the genus Clostridium. Another interesting observation in this regard was made by Untawale and McGinnis (1979). These researchers indicated that depressed growth of the growing chicken caused by the substitution of rye for corn in the diet was associated with an increased microbial adhesion to the intestinal mucosa.

In spite of many attempts to explain the mode of action of antibiotics on growth, the exact mechanism of growth-promoting effect of antibiotics is still a matter of speculation. However, the fact that antibiotics differing widely in chemical properties still exert similar growth-promoting effects indicates that the mode of action in growth promotion likely involves an influence on the intestinal microflora. In addition, antibiotics are known to reduce the intestinal weights of the chicken (Coates et al., 1955; Jukes et al., 1956). More in depth studies are needed regarding the influence of rye and/or dietary fiber on the intestinal microflora which is known to influence mucosal morphology and epithelial renewal in the chicken (Cook and Bird, 1973; Rolls et al., 1978). The effects of antibiotics and water treatment of grains on this matter should also be investigated.

II. Sticky and/or Watery Droppings Phenomenon in Poultry

A. Introduction

In spite of the repeated observations made in many laboratories, there have been only limited efforts to tackle the problem of sticky and/or watery droppings among chickens fed diets based on rye or barley. In addition to the well-known low nutritive value of these grains relative to corn or wheat, this unique nature of rye and barley presents a management problem that further restricts their use in diets for poultry. This peculiar phenomenon of sticky and/or watery droppings is therefore an important aspect worthy of in depth study if the problems of feeding rye to poultry are to be fully understood. Besides the dietary-originated sticky and/or watery droppings in chickens, non-dietary origin wet droppings conditions in laying flocks have been reported by a few workers but the cause of the latter type is not known. Fiber and particularly the water-soluble component of fiber in the diet is believed to be a causative agent in the former type of sticky and/or watery droppings.

B. Rye and barley as sources of water-soluble dietary fiber

In a series of studies of the gross yields of unfractionated water-soluble gum-like materials from a number of cereals, Preece and McKenzie (1952) found that barley and rye yielded 1.34% and 1.05% gum-like polysaccharides, respectively. It was clear that the gums from different cereals differed markedly in yield, in chemical nature, and in physical properties. Barley appeared to be the best source of β-glucosan and rye the best source of pentosan. Recently, Antoniou (1980) reported that rye grain contained about 2.1% soluble pentosans and 7.9% water-insoluble pentosans. These carbohydrate fractions were composed mainly of xylose and arabinose with minor quantities of mannose, galactose and glucose.

The principal reason for the importance of the pentosans and β-glucans in terms of nutrition is their hydrocolloidal properties. Hydrocolloids, being partially soluble in water, can bind large amounts of water forming clear viscous solutions or gels (Neukom, 1976). In addition, most of the hydrocolloids are known to be resistant to the digestive enzymes of the host animal (Hawkins and Yaphe, 1965; Sharratt and Dearn, 1972). According to the recent definition of Trowell et al. (1976), the dietary fiber includes all the polysaccharides and lignin in the diet that are not digested by the endogenous secretions of the animal. Therefore, pentosans and β-glucans can be designated as water-soluble dietary fiber. The antinutritional properties of the water-soluble dietary fiber becomes manifest when chickens are fed diets based on rye or barley which contain high concentrations of pentosans and β-glucans, respectively, as reviewed above.

C. Sticky and/or watery droppings in relation to diets high in water-soluble dietary fiber

Burnett (1966), in studying the sticky dropping phenomenon and poor performance among birds fed barley, hypothesized that hemicellulose and related substances give rise to a very viscous state when present in the alimentary tract of the birds. Low-enzyme barley containing an inherently low β-glucanase activity produced the greatest response in this regard. Gohl et al. (1978) also reported that the sticky dropping problem could be alleviated by water treatment of barley prior to feeding or by the addition of β-glucanase to the diet. It was, therefore, suggested that water-treatment allowed hydrolysis of barley gums by endogenous enzymes.

One of the consistent features noted when using rye in poultry diets has been the production by the birds of wet and extremely sticky droppings. The effect would appear to be similar to that described for barley-fed birds. When diets containing 15% or more of rye were fed to the chicken, a characteristic "sticky" excreta occurred (Halpin et al., 1936a). North (1933) reported that rye had a laxative effect on hens but did not appear to be injurious to health. Fernandez et al. (1973b) observed that acetone extraction of rye had no effect on the growth depressing properties of the grain or on the sticky excreta condition associated with its use in poultry feeding. Chickens receiving diets containing water-extracted rye grew significantly better and demonstrated better feed conversion efficiency than did birds fed untreated rye. Furthermore, excreta condition was significantly improved among birds fed the water-extracted rye, and the dried water extract from rye caused the sticky excreta condition when added to a diet containing corn. It was concluded, therefore, that a factor(s) present in rye causing the sticky excreta condition when fed to chickens can be extracted by a simple water extraction process.

There have been some attempts to ameliorate the sticky excreta condition among rye-fed birds other than by water treatment. Young chickens fed a 55% rye diet supplemented with various antibiotics at a concentration of 55 ppm grew better than did chickens fed a basal diet (Wagner et al., 1978). However, all chickens fed the rye diets exhibited a sticky excreta condition regardless of the presence of antibiotics in the diet. Exposure to gamma irradiation, procaine penicillin or pectic enzyme supplementation improved the growth of chickens fed rye diets (Patel et al., 1980). These treatments, however, had no significant effect on the excreta condition of birds fed diets based on rye. These workers indicated that the component of rye that causes sticky excreta is not changed by gamma irradiation and/or pectic enzyme, and therefore, is different from the growth depressing factor.

In conclusion, water-soluble dietary fibers present in rye and barley appear to be the cause of depressed growth and sticky and/or watery droppings of chickens fed diets based on these grains. Improved growth response of young chickens fed rye diets, however, can be achieved without affecting the water-soluble dietary fibers present in rye. In this case, the birds keep producing sticky droppings. Further research is needed to establish the relationships among growth depressing properties of rye, the sticky and/or watery droppings phenomenon and the water-soluble dietary fibers present in rye.

D. Wet droppings due to non-dietary origin

Osbaldiston (1969) and Lintern-Moore (1972) described the condition known as wet droppings in laying flocks. This condition was not associated with diet. It was characterized by normal feed consumption and egg production, with birds clinically healthy but excreting liquid droppings. It appeared to be transient, reversible and occurred in only a few hens with the remainder of the flock continuing to produce normal droppings. Wet droppings were not associated with a particular breed or any change in diet or drinking water. Water and electrolyte balance studies were carried out with birds showing wet droppings (Osbaldiston, 1969; Lintern-Moore, 1972). It was concluded that wet droppings were the direct result of a primary polydipsia (psychogenic in origin) rather than an obligatory loss of body water followed by an increased water intake. However, it was not specified whether wet droppings was due to an increase in urine or fecal water in these studies, which makes the conclusion drawn less convincing. More in depth studies are needed to understand the sticky and/or wet droppings phenomenon, regardless of whether it is dietary in origin or psychogenic in origin. Surgically modifying the bird to facilitate the separate collection of urine and feces might be useful to elucidate the cause of wet droppings.

III. Water and Electrolyte Metabolism in Chickens

A. Introduction

Since the avian kidney has long been considered to function in principle like that of mammals, water and electrolyte metabolism in general and especially the renal aspects thereof is an area which has not been much emphasized (Sykes, 1971). Studies of the water and electrolyte metabolism and of renal function by nature involve collection of urine. Unfortunately, the collection of urine in birds presents a special challenge because of the intimate relationship between urine and feces as expelled normally from the cloaca. Moreover, there is some doubt about the physiological validity of the findings when steps are taken to separate urine from feces. Nevertheless, this separation of urine and feces is necessary as Medway and Kare (1959) remarked that, "a study of water metabolism is not complete until one equates the water intake with that lost from the body through all routes". A prerequisite in this kind of study is that special care be given to data interpretation in experiments that involve urinary separation, diuretics, anesthesia, length of collection period, or methods of restraint that requisite abnormal postures of the birds (Sykes, 1971).

B. Factors affecting water consumption of the chicken

According to Medway and Kare (1959), the milliliters of water drunk per gram of feed consumed ranged from 2.1-2.6 in growing chickens of 1-16 weeks of age. In 32-week-old laying hens, the amount was 3.6 ml/g of feed. Barott and Pringle (1947) found that chickens on the ninth day after hatching drank approximately 1.6 g of water for each gram of feed consumed. Pursuing this study further, Barott and Pringle (1949) found that chickens on the 18th day after hatching drank approximately 1.55 g of water for each gram of feed consumed. The amount of water consumed by a White Leghorn laying hen was reported by Heywang (1941) as approximately 18.2 gal per year. It was further stated that the amount of water consumed increased with increases in air temperature, live weight and rate of lay. It can be easily understood, therefore, that the age of the bird is just one example out of many factors affecting water consumption.

Several other factors have been found to affect the amount of water consumption in the chicken. Kare and Biely (1948) found that the addition of increasing amounts of salt to the diet caused a progressive increase in water intake per gram of feed consumed. Similar observations were made by Kondo and Ross (1962b). Increasing the protein content of the feed was found to increase the water consumption (James and Wheeler, 1949; Wheeler and James, 1950). Patrick (1955), in studying the same relationship, found that increasing the protein content of the feed did not always increase water consumption but in some instances actually decreased it. The feed particle size was found to have no effect on water or feed consumption, moisture content of the droppings, or weight gains (Eley and Hoffmann, 1949).

As reviewed above, many research workers have conducted experiments to study the factors affecting water consumption in chickens. In many cases, however, studies were done superficially, not looking into the basic mechanisms involved in the changes in water consumption. Any change in water consumption invariably resulted in a similar change in water excretion, and vice versa. For this reason, concomitant in depth studies about the pattern of water excretion are needed in order to get more insight into the factors affecting water consumption of the chicken.

C. Post-renal modification of urine

The function of the cloaca and colon (rectum) in regulating the excretion of urinary water in the fowl has been an active area of research for the past four decades. In many cases, however, the information obtained has been inconsistent and very often contradictory owing to the diversified techniques employed among the different experiments. To make the matter worse, interpretation of the data obtained or observations made was done improperly from time to time. Therefore, caution is necessary when reviewing the published reports in this area.

Cloacal reabsorption was first examined critically by Korr (1939) who believed that urine could make retrograde movement from the cloaca into the colon where water reabsorption occurred. This view has been substantiated with the aid of radiographs following intravenous injection of radiopaque contrast media which are rapidly excreted into the urine (Koike and McFarland, 1966; Akester _et_ _al_., 1967; Nechay _et_ _al_., 1968). The absence of a distinct anatomic sphincter between the cloaca and colon of the chicken (Calhoun, 1954) adds credence to this view. Weyrauch and Roland (1958), however, concluded from a study involving radiography that valvular folds at the junction of the colon and cloaca prevented reflux of a barium mixture from the cloaca into the colon. It should be mentioned here, however, that this experiment was done with hens under ether anesthesia; the conclusion might have been reversed had unanesthetized birds been used. In studies on the economy of water and electrolytes in the fowl, the significance of retrograde movement of urine in relation to functional post-renal reabsorption must be examined thoroughly before conclusions are drawn.

Most of the evidence for post-renal reabsorption of water has been based on the increase of urine volume after separation of the urinary and alimentary tracts (Korr, 1939; Hart and Essex, 1942; Dicker and Haslam, 1966). That absorption of ureteral water occurs in the normal bird, however, has not been supported by other workers. In a study designed to measure indirectly water absorption from ureteral urine in the cloaca and colon of the hen, Dixon (1958) separated urine from feces by surgical exteriorization of either the ureters or the colon. The data obtained indicated that little water was reabsorbed from the ureteral urine in the cloaca and colon of the hen. Skadhauge and Schmidt-Nielsen (1965) reported that no marked change in urine occurred post-renally in roosters subjected to various types of osmotic stress, i.e., dehydration, water and salt loading. Nechay and Lutherer (1968) investigated the contribution of the cloaca to post-renal salt and water reabsorption by comparison of urine collected directly from one kidney with urine collected simultaneously from the other kidney after passage through the ureter and cloaca, but not through the colon. To achieve this, a ligature was placed just above the cloaca to prevent reflux of urine into the colon; consequently it was impossible to assess the role of the colon in post-renal modification of urine. The data indicated that in the cloaca-ureter area only passive absorption of water occurred. Since this absorption was from a urine that was hypotonic to plasma, it may be suggested that the cloaca does not play an active role in the water economy of the chicken. Weyrauch and Roland (1958) placed either radiosodium or radioiodine in the cloaca of birds that had the anus sealed off from the rest of the intestinal tract and analyzed the radioactivity of blood to estimate the absorption of these elements. It was concluded from these experiments that electrolytes are not absorbed from the urine contained in the cloaca. The majority of the evidence available to date indicates that the role of the cloaca, per se, in water metabolism is a minor one.

The reabsorption of salt and water in the cloaca and colon of the chicken was investigated by means of an in vivo perfusion technique (Skadhauge, 1967). Water was observed to move against an activity difference of 65 mosms. It was claimed that a reabsorption of 3% of ureterally voided water during hydration, and 4% of ureterally voided salt during salt loading took place in the cloaca. Furthermore, 50% of the sodium and perhaps $\geq$15% of the water was reported to be reabsorbed in the cloaca. However, according to the design of the perfusing system used in the experiment, not only the cloaca but also the colon were perfused with the perfusing solutions tested. Therefore, it might not be correct to state that the reabsorption occurred only in the cloaca. Since, as previously described, the cloaca appears to play a minor role in the water economy of the chicken, it would be more reasonable to assume that the colon plays a major role in the post-renal reabsorption of salt and water rather than the cloaca.

Hart and Essex (1942) conducted a thorough study on water metabolism of the chicken. The separation of urine from feces was achieved by colostomy or by exteriorization of the ureters. In this study with hens that had exteriorized ureters, it was found that the addition of 1% salt to the diet was required to maintain the birds in excellent health for an extended period of time. Because of this fact and since severely dehydrated birds could be restored to normal simply by adding salt to the diet, it was concluded that reabsorption of electrolytes and water from ureteral urine in the colon of intact birds is the only mechanism of importance in normal water economy of the chicken. When drinking water was withheld, colostomized birds lost body weight more rapidly than did intact birds due to dehydration, indicating that normally some ureteral water is reabsorbed from the colon. In addition, if 1% salt was not added to the diet of colostomized birds, an increase of water intake always occurred. Although the original authors could not explain these observations, it might be speculated that the additional salt aided water reabsorption at the kidney level.

When colostomized hens were fed a diet lacking in sodium, potassium and chloride, a 3-fold increase over controls in water intake and excretion occurred (Lumijarvi _et al_., 1967). However, when the comparisons were made with intact birds, only 2-fold increases in water intake and excretion were observed (Hill and Lumijarvi, 1968). In contrast, water intake and excretion were quite similar in intact and colostomized hens fed diets containing adequate levels of electrolytes. These data indicate that renal function was impaired by electrolyte deficiency as discussed above, and that the rate or extent of electrolyte depletion was increased in colostomized hens. In this study fasted intact hens reduced water intake to 25% of normal. In contrast, fasted colostomized hens, on the average, showed increased water intake and urine volume and considerable individual variation in response; about half of the number of hens used showed markedly increased water turnover. These data again indicate a response to electrolyte depletion. Assuming that impaired colon function is the only difference between intact and colostomized hens, these observations were interpreted by the authors to indicate that the colon normally functions to conserve electrolyte under marginal or depleting conditions. It should be realized, however, that colon function is impaired not by the colostomy operation, per se, but by the fact that urine is prevented from reaching the colon due to the separation of the urinary and alimentary tracts. Post-renal reabsorption of urine could then not occur in the colon of colostomized hens.

The extent of post-renal reabsorption of salt and water appears to be dependent upon many factors, i.e., the reabsorption capacity of the epithelium of the coprodeum and large intestine, the rate of urine flow and the degree of dehydration and salt depletion. A limited reabsorption of urinary salt and water in the cloaca and colon was suggested during dehydration even though the ureteral urine was hyperosmotic to plasma (Skadhauge, 1968; Bindslev and Skadhauge, 1971). In a review article, Skadhauge (1977) described that in birds exposed to hydration only 2.3% of the ureterally excreted water was reabsorbed post-renally during the sojourn of the urine. Similarly the post-renal salt reabsorption in the salt-loaded state was calculated to be only 2% of the ureterally excreted load. In a dehydrated state, however, approximately two-thirds of the salt and a small amount of water (≃14%) was reabsorbed, even though the ureteral urine was hypertonic to plasma (Bindslev and Skadhauge, 1971). These same workers estimated that net salt absorption in normal birds was accompanied by a water absorption of 1.1 μl/μeq Na^+ in the absence of a transmural osmolality difference. In dehydrated birds the value augmented to 1.5 μl H_2O/μeq Na^+ but the reason and/or mechanism of this adaptation was not clear.

D. Countercurrent system in avian kidneys

The kidney of the bird as that of the mammal has loops of Henle and medullary cones. This loop dips down into the medullary tissue and forms the basis for the countercurrent multiplier which allows the creation of a local area of very high osmotic concentration (Poulson, 1965). Hypertonic urine is formed as a result of fluid in the collecting ducts coming into equilibrium with this osmotic gradient, but, as a consequence of a relatively poor development of this section of the nephron, the fowl is not able to produce very hypertonic urine. In the domestic fowl, the average urine-to-plasma ratio for osmotic concentration ranges from about 0.3 in the hydrated to 1.6 in the dehydrated state (Skadhauge and Schmidt-Nielsen, 1967a). The osmotic concentrations vary from 50 mosm/ℓ up to 600 mosm/ℓ; the latter being equal to about twice the plasma concentration. These values are considerably lower than those found in many mammals. The kidney of the fowl contains relatively few nephrons that possess a long loop of Henle. Poulson (1965) reported that in terrestrial birds the capacity to conserve urinary water by producing a concentrated urine was directly related to the number of Henle's loops in the kidneys. In contrast, urine concentrating ability in mammals is determined by the length of the long Henle's loops and not by the number of nephrons having long Henle's loops (Schmidt-Nielsen and O'dell, 1961).

Skadhauge and Schmidt-Nielsen (1967b) provided experimental evidence of countercurrent concentration in the fowl by analyses of cortical and medullary tissue obtained after rapid freezing _in situ_. In dehydrated fowl, the osmotic pressure was 413 mosm/kg tissue water in the cortex, 467 in the medulla and 542 in the urine. It is interesting to note from this work that the hydrated fowl while excreting a hypotonic urine (167 mosm/kg H_2O) had hypertonic osmotic pressures in the cortex and medulla (432 and 375 mosm/kg H_2O, respectively).

The avian kidney, like mammalian kidneys, has the ability to secrete a dilute urine. Since the tubular fluid becomes very hypotonic as it leaves the ascending limb of the loop of Henle, a dilute urine can be excreted simply by allowing this fluid to empty directly into the ureters. A mechanism exists in the kidney for this type of excretion (Guyton, 1976). The distal tubules of the fowl's kidney, like that of the mammals, are very poorly permeable to water. Also, in the absence of antidiuretic hormone, the epithelial cells of the collecting tubules are almost completely impermeable to water. Therefore, in the absence of this hormone no water is absorbed from the distal tubules and collecting ducts. The dilute tubular fluid from the ascending limb of the loop of Henle then flushes rapidly into the ureters.

The mechanism of excreting a concentrated urine is exactly the opposite to that for excreting a dilute urine. Large quantities of antidiuretic hormone are secreted into the body fluids in response to the elevated plasma osmotic pressure. The avian kidney is sensitive to the antidiuretic hormone which greatly increases the permeability of the collecting ducts to water resulting in the production of a concentrated urine. As a result of extra water reabsorption from the collecting ducts, the previously elevated plasma osmotic pressure returns to normal signaling the posterior pituitary gland to stop releasing the antidiuretic hormone.

E. Active absorption of sodium and solute-linked water flow across the epithelium

The epithelium of the coprodeum and large intestine of the domestic fowl is exposed to ureteral urine since the urine is moved retrogradely into these parts of the intestinal tract as reviewed previously. It was of particular interest to note that in dehydrated birds considerable amounts of salt and water were reabsorbed from ureteral urine even though the urine was considerably hypertonic to plasma (Skadhauge, 1967; Skadhauge, 1968). Since the absorptive epithelium is exposed to fluids of differing osmolality, the coprodeum and large intestine are suitable for the study of the transepithelial solute-linked water flow.

In studies with rat ileum, Curran and Solomon (1957) have proposed that water transport by the intestine is a passive process resulting from active solute transport. Later, Parsons and Wingate (1961) found in an *in vitro* preparation of rat intestine that water could be transported from the mucosa to the serosa even though the solute concentration of the mucosal solution was greater than that of the serosal solution. This net transport of water against a concentration gradient appeared to be the result of the active transport of water (Grim, 1962). However, Curran (1960) has proposed a mechanism which could account for this observation in terms of passive water movement coupled with active solute transport. This view was supported further by a model system for biological water transport (Curran and MacIntosh, 1962).

Mongin *et al*. (1976) measured the osmotic pressures along the digestive tract of the domestic fowl. In the hen osmotic pressures were: crop 537; gizzard 312; duodenum 571; proximal jejunum 650; distal jejunum

573; proximal ileum 574 and distal ileum 451 mosm/kg H_2O. In the cockerel osmotic pressures in the alimentary tract followed the same pattern as in the hen. Absorption of water across the digestive tract seemed to be achieved therefore against a concentration gradient. According to Skadhauge (1968), the average osmolality of the contents of the coprodeum ranged from 489 mosm to 143 mosm in the dehydrated and hydrated states, respectively. Similarly, it ranged from 376 mosm to 192 mosm in the dehydrated and hydrated states, respectively, in the colon. In these areas, where an absorptive epithelium is present, sodium chloride absorption is regulated by the salt balance of the bird (Skadhauge, 1976).

As reviewed above, water absorption in the intestine is a passive process resulting from active solute transport. In the coprodeum and large intestine of the domestic fowl, where the absorptive epithelium is exposed to ureteral urine, a significant fraction of ureteral water may be absorbed against a concentration gradient. The extent of this solute-linked water absorption from ureteral urine depends largely on the water and salt balance of the birds.

F. Diuresis in the fowl

Physiologically, diuresis can be classified into three different types; (1) that caused by an increased glomerular filtration rate, (2) that caused by an increased tubular osmotic load, and (3) that caused by an inhibition of the secretion of antidiuretic hormone. Although changes in urine flow can be brought about by changes in filtration rate, normal variations in urine flow are effected largely by changes in water reabsorption, not by changes in filtration rate (Pitts, 1974). Osmotic diuresis is caused by an increased tubular osmotic load. It occurs when any non-reabsorbed osmotic substance passes through the tubular system into urine and acts osmotically inside the tubules to prevent water reabsorption. This happens when excess salt is ingested by the animal. On the other hand, the third type of diuresis can happen in the animal fed diets deficient in salt. It has been well established that the avian kidney is sensitive to antidiuretic hormone (ADH) and that this hormone is released from the fowl's posterior-pituitary gland in much the same way as in mammals (Sykes, 1971). The major function of ADH is to control the permeability of distal tubules and collecting ducts to water in response to the changes in plasma osmolality. The secretion of ADH is inhibited in birds fed diets deficient in salt due to a decrease in plasma osmolality to below normal levels. In the absence of ADH, the permeability of distal tubules and collecting ducts to water becomes very poor allowing copious flow of urine and hence diuresis.

In an early study on water metabolism of the chicken, Hart and Essex (1942) observed that birds with exteriorized ureters fed a diet without added salt lost body weight rapidly presumably due to extreme dehydration. This weight loss persisted in spite of increased water consumption but could be counteracted by the addition of 1% salt to the diet. Perhaps because urine volumes were not recorded with these birds, the authors did not identify the symptoms as diuresis. It appears that birds with an artificial anus or exteriorized ureters are much more prone to diuresis than are intact birds.

In studies relating to diuresis in the domestic fowl, Dicker and Haslam (1966) also observed an increased ratio of water intake to food intake after the exteriorization of the ureters. Water diuresis was induced artificially by administering 50 ml of water with the aid of a stomach tube. Immediately after water gavage, there was a sharp rise of urine flow accompanied by an increase in endogenous creatinine excretion and a fall in the osmolarity of the urine. This initial increase in urine flow was of short duration, and was followed by a normal pattern of diuresis with a peak in urine flow at about 90 min after hydration. The first rise in urine flow following the filling of the crop appeared to be of reflex origin, as distension of the crop with paraffin produced an enhanced excretion of urine and creatinine.

Koike and Lepkovsky (1967) produced permanent polyuria by lesions in the chicken hypothalamus. The low levels of arginine-vasotoxin (AVT; the avian ADH) in the posterior pituitaries of the lesioned birds indicated primary polyuria, however, the occurrence of crops distended with water in some chickens also suggested a primary polydipsia. Both lesioned and non-lesioned chickens were colostomized to collect urine. The urine from the lesioned chickens was markedly hypotonic (29 mosm/kg H_2O), and that of the non-lesioned chickens was slightly hypotonic (106 mosm). It is of interest here to note that the diet used in this experiment contained only 0.6% salt, a level somewhat lower than that used by Hart and Essex (1942) to prevent diuresis in colostomized birds as discussed above.

In an experiment reported by Lumijarvi *et al.* (1967), colostomized hens fed a purified diet supplemented to contain 127 meq Na/kg, 136 meq K/kg and 242 meq Cl/kg consumed 70-120 ml water/kg/day and excreted 45-70 ml urine/kg/day having an osmolality of 390-480 mosm/kg H_2O. Restriction of Na, K and Cl to basal levels (20 meq Na, 2 meq K and

6 meq Cl/kg) increased water intake and urine volume to 235 and 185 ml/kg/day, respectively, and decreased urine osmolality to below 50 mosm/kg H_2O. Sodium or chloride restriction alone caused an intermediate increase in water intake and urine volume and a decrease in urine osmolality. Potassium restriction alone had no effect on water turnover but caused a small decrease in urine osmolality. The onset of changes in water turnover were rapid, occurring 2-4 days after the initiation of restriction and were accompanied by either no change or a reduction in plasma osmolality and an increased hematocrit. These results indicate that sodium and chloride are required for maintenance of normal water balance and/or antidiuresis in the chicken.

As already indicated, the addition of salt at levels above the normal requirement level to the diet of diuretic birds reduces water loss from the body by decreasing urine volume. This indirectly reduces water consumption. On the other hand, excess salt or solutes in the diet of non-diuretic birds would likely increase water consumption. Frank _et_ _al_. (1967) studied the influence of dietary solute concentration upon water consumption in chickens. Average fluid intake was increased 2.7 and 1.8 ml/mosm of solute ingested for sodium chloride and urea, respectively, regardless of the concentration fed. In addition, the effect was additive when the solutes were ingested in combination. The data indicated that excess salt or solutes in the diet of intact, non-diuretic birds may stimulate the rate of water turnover due to osmotic diuresis. Skadhauge and Schmidt-Nielsen (1967a) also observed osmotic diuresis in roosters during salt-loading. The urine was slightly hyperosmotic to plasma and the urine flow was high.

Harris and Koike (1977) examined the effects of chronic dietary sodium restriction, with and without the administration of a diuretic (furosemide) in the domestic fowl. Food intakes were similar among the treatments employed, but water intakes tended to increase with the administration of the diuretic. No differences were observed in arterial pH, plasma osmolality or in the plasma concentrations of potassium or chloride. Plasma Na levels were higher among birds on the control diet in comparison with those administered the diuretic and fed either the control or Na-deficient diets. The low Na diet and/or diuretic treatment were associated with reductions in the volumes of extracellular fluid (ECFV) and interstitial fluid (ISFV). Plasma volume (PV) and hematocrit, however, remained unchanged. A lack of correlation between PV and ECFV or ISFV indicated that the chicken has the ability to maintain vascular volume over ranges of Na depletion that are associated with hypovolemia in mammals. Djojosugito et al. (1968) and Wyse and Nickerson (1971) examined the mechanisms responsible for the more efficient volume restoration after hemorrhage in birds as compared with mammals. The data indicated that considerable differences exist between birds and mammals. It was concluded that the greater resistance to blood loss and shock of most bird species as compared with mammals is probably directly related to their much greater capacity for fluid mobilization from the skeletal muscles. Undoubtedly the maintenance of PV in response to reduced intake of sodium in chickens depends on the extent to which body sodium is depleted. Hypovolemia, indirectly assessed by hematocrit, was readily induced, however, in rapidly growing birds on a chloride- (Leach and Nesheim, 1963) or sodium-deficient (Lumijarvi and Vohra, 1976) diet.

It appears, therefore, that the ability to maintain PV is also dependent on the maturity of the birds, with younger birds being less effective.

In summary, the avian kidney functions similarly to the mammalian kidney to maintain normal economy of water and salt. Diuresis and/or antidiuresis is one of the essential functions of the kidney. When excess solutes are fed, osmotic diuresis occurs. On the other hand, when the birds are fed diets deficient in salt, diuresis also occurs due to the inhibition of ADH secretion in response to a lowered plasma osmolality. Birds with an artificial anus or exteriorized ureters are more prone to diuresis than are intact birds, indicating the essential function of colon to conserve water and electrolytes under marginal or depleting conditions. Experimental results also indicate that birds are more capable of maintaining plasma volume by mobilizing fluid from the skeletal muscles than are mammals.

G. Renal retrieval of salt

Urine consists of the excretory products of the body after blood has gone through the processes of glomerular filtration, tubular reabsorption and tubular secretion in the kidney. The essential function of the kidney is to adjust the degree of contribution of each of these processes to urine formation so that the animal body can maintain homeostasis. Rigorous proof of the contributions of each of these discrete renal processes is of relatively recent origin, the major evidence having accumulated over the past 40 years.

Several early workers conducted experiments with rats on the deficiency symptoms of sodium, potassium and chloride. The findings from these experiments indicated that the process of tubular reabsorption played a prominent role when the animals were deficient in these elements. Orent-Keiles and McCollum (1940) found that sodium retention was negative even though urinary sodium excretion was reduced to a very low level when rats were fed a diet extremely deficient in sodium. During the experimental period the average body weight gain of rats on the Na-deficient diet was 57.7 gm and that of the controls was 97.5 gm. Nitrogen balance figures indicated that the rats deficient in sodium did not have the ability to utilize protein as efficiently as did controls. The most striking effect of the sodium deficiency was on potassium, which showed a marked retention.

Potassium deficiency symptoms were studied with rats by the same workers (Orent-Keiles and McCollum, 1941). A potassium deficient diet permitted growth but at less than the normal rate. The urinary excretion of potassium reduced to a level of zero. Although there were no differences in nitrogen or sodium balances, magnesium storage was more than 2.5 times greater in the rats on the low-potassium diet. The chloride balance of rats on the low-potassium diet was negative, indicating a relationship between potassium and chloride.

Greenberg and Cuthbertson (1942) found that the rats fed a chloride deficient diet gained less and ate more food per gram of gain in body weight than did controls. The whole blood chloride values in the chloride-deficient rats were significantly lower (252 mg %) than those of controls (295 mg %). The animals were able to conserve chloride by reducing urinary output and this response occurred within a few hours of the onset of the experiment.

As reviewed above, the rat kidney has the ability to retrieve sodium, potassium or chloride by the process of tubular reabsorption when these ions are deficient in the diet. This explains why the intake of these ions must be drastically reduced to produce an actual deficiency. Little or no data has been reported in this regard for poultry but it would appear that the avian kidney has a similar ability of renal retrieval of salt.

IV. Factors Affecting the Salt Requirements of Poultry

A. Introduction

Sodium is the chief cation of extracellular fluid. On the other hand, potassium is the chief cation of intracellular fluid. All living things, both plant and animals, require these elements for normal metabolism. Sodium, potassium and chloride function with phosphates and bicarbonates to maintain homeostasis, osmotic relationships, and an optimum pH throughout the body. These minerals also function in controlling the passage of nutrients into cells, and in water metabolism in general. The animal body has a special ability to conserve its supply of these minerals by decreasing excretion when the intake is limited. A deficiency of any of these minerals results in lack of appetite, a depressed growth rate, loss of weight and production performance in the adult - general symptoms which reflect more specific physiological and pathological changes for each.

B. Salt requirements of poultry and interrelationships with other minerals

Experimental evidence on the amount of salt required by chickens varies considerably. Halpin et al. (1936b) reported that 0.5% added salt meets all needs for growth or production and maintenance in the growing chickens or laying hens. On the other hand, Barlow et al. (1948) claimed that 1% added salt was optimum in growing chickens, growth being superior to that of groups receiving 0 and 0.5%. Levels of 2 and 3% added salt resulted in growth which was neither better nor worse than the 1% level. Heuser (1952) conducted an experiment with growing chickens to estimate the optimum level of dietary salt. Using a basal diet containing 0.41% salt, the total minimum salt requirement in this experiment was approximately 0.65 percent. It was, therefore, concluded that the addition of 0.25% of salt was sufficient in this experiment. The minimum requirements for sodium and potassium by chicks fed semipurified diets for the first few weeks of life were found to lie between 0.10-0.30% and 0.23-0.40%, respectively, the higher levels being required for maximum growth (Burns et al., 1953). The level of potassium appeared to have no effect on the sodium requirement, provided it was not at a limiting level. The requirement for chloride was found to be less than 0.06%, and thus lower than its equivalent of the amount of sodium required. McWard and Scott (1961) reported that the sodium requirement for optimum growth of the young chicken, fed an isolated soybean protein diet, was 0.11% of the diet. These same workers found that on a casein-gelatin diet, formulated to simulate the diet used by Burns et al. (1953), the requirement for sodium was 0.2% of the diet. It was concluded that the physical properties of the basal diet employed by Burns and coworkers were largely responsible for the chicken showing a response to supplemental sodium up to a level of 0.3%. It appears that the sodium requirement of the chicken varies depending on the type of diet being fed.

Recently the sodium and chloride requirements of broiler chickens have been re-examined in view of the interaction between these ionic components of the diet in the acid-base balance of the body (Hurwitz et al., 1973). Blood pH was found to be a sigmoidal function of the dietary ratio of Na/Cl. The requirements of sodium and chloride were interdependent; optimal growth occurred with a Na/Cl ratio (w/w) of unity. The moisture score of the droppings indicated a positive dependence of the moisture on the total dietary sodium and on the Na/Cl ratio. With increasing levels of an optimal Na-Cl mixture in the diet, body weight gain increased linearly to reach a peak with a diet containing 0.13% sodium and 0.13% chloride. Cohen et al. (1972) tested a hypothesis which ascribed to dietary sodium and chloride the role of alkalogenic and acidogenic agents, respectively. Blood pH and HCO_3^- were a function of the dietary Na/Cl ratio, regardless of total concentrations of the two ions in the diet. With a constant dietary level of chloride, alkalosis was produced with $NaHCO_3$, Na_2SO_4, CH_3COONa, and NaH_2PO_4 as dietary sodium supplements. Conversely, with a fixed level of dietary sodium, acidosis was produced by $CaCl_2$, $FeCl_3$, KCl and choline chloride as chloride supplements. These results confirmed the hypothesis that the dietary sodium and chloride act as alkalogenic and acidogenic agents, respectively, in the body fluids.

Lumijarvi and Vohra (1976) studied the response of Japanese quail fed a purified diet to dietary increments of sodium chloride. Birds fed a basal diet (0.042-0.051% Na) displayed poor growth, high mortality, depressed plasma sodium levels, elevated blood hematocrit and increased relative adrenal gland weights. Growth approached a plateau and the other parameters reached normal values at a total dietary sodium level of 0.1%.

Kumpost and Sullivan (1966) reported that turkeys, 0-4 weeks of age, required 0.15 to 0.20% of dietary sodium for maximum performance. There was a significant interaction between sodium and potassium relative to body weight gain. When the lowest level of sodium (0.08%) was fed, body weight gains were increased with graded increments of potassium up to 0.37%. Likewise, when the lowest level of potassium (0.17%) was fed, body weight gain increased with graded increments of sodium. These elements, therefore, appeared to spare or replace each other within limits of 0.08% dietary sodium and 0.17% dietary potassium. An optimum ratio of about 2.0 or 2.5 parts of potassium to one part of sodium in the diet of young turkeys was indicated. Leeson _et al_. (1976) reported that at least 0.2-0.3% salt should be provided in the diet of young poults for maximum growth.

A series of experiments were conducted on the dietary relationship of the cations, sodium and potassium, and the anions, chloride and sulfate (Nesheim _et al_., 1964). The data showed that excesses of dietary chloride or sulfate ions markedly depressed the growth of chickens unless these anions were balanced with equimolar levels of dietary sodium or potassium. Excess sodium was also detrimental unless a high level of chloride was present. Chicks tolerated excesses of potassium better than excesses of sodium.

Considerable attention has been given to the movement of sodium and potassium in cellular systems in general and across the intestinal wall in particular. On the basis of _in vitro_ and _in situ_ studies, sodium is believed to be actively transported across the intestine (Curran, 1965).

With regard to potassium, studies indicate that this ion is transported passively across the jejunum and ileum (Clarkson, 1967; Gilman _et al._, 1963). The relationships between sodium ion and potassium ion concentrations in the intestinal contents and the net absorption of these ions were studied in laying hens fed diets containing either high (0.15%) or low (0.07%) levels of sodium (Hurwitz _et al._, 1970). A large net secretion of cations, especially Na^+, occurred in the upper gastrointestinal tract, regardless of diet. Sodium ion absorption occurred along the entire small intestine, whereas potassium ion was absorbed in the jejunum but secreted in the ileum. In the ileum, Na^+ absorption and K^+ secretion were greater in the low- as compared to the high-sodium birds. Consequently a reciprocal relationship between the concentrations of the two cations in this segment was evident. The results also indicated that Na^+ was always absorbed against a concentration gradient, and K^+ along the respective gradient of potassium. Potassium ion was secreted against its gradient into the ileum.

The interrelationships among dietary concentrations of sodium, potassium and chloride in laying hens were studied (Sauveur and Mongin, 1978). It was found that a deficiency of sodium (0.5 g Na/kg) was aggravated by the restriction of chloride (0.8 instead of 1.4 g/kg), but was partly compensated for by supplementing the diet with potassium (12 instead of 7 g/kg). Without a sodium deficiency other interactions occurred; for example, the higher concentration of potassium became unfavorable if the other two ions were also supplied at the higher concentrations. These results indicated that, for the laying hen, the optimum concentrations of sodium, potassium and chloride cannot be determined independently but depend upon the concentrations of the companion ions in the diet.

Dietary calcium and phosphorus levels were found by Slinger _et_ _al_. (1950) to influence the salt requirement of the growing chicken. With diets deficient in calcium or phosphorus, the salt requirement was low. Response to increasing dietary phosphorus suggested a sparing effect between this mineral and salt. McCuaig and Motzok (1974) also reported that an excess of dietary salt enhanced bone mineralization when dietary phosphorus was adequate, and it tended to counteract the effects of a phosphorus-deficient diet. However, high calcium seemed to be antagonistic to the salt response (Slinger _et_ _al_., 1950). Some evidence was also found by the same workers that salt increased the dietary requirement of manganese for perosis prevention.

As reviewed above, the amount of sodium chloride required in the diet of the fowl for optimum growth and production is subject to considerable variation due, in part, to the significant interrelationships of salt with other minerals, i.e., potassium, calcium, phosphorus and manganese, etc. In addition, the salt requirement is known to be influenced by the types of diets being fed to the birds. More in depth research is required to elucidate the mechanisms causing these interrelationships.

C. Influence of "fiber" on the salt requirement of the chicken and on the route of sodium excretion

An interaction of great interest from the viewpoint of the present thesis was found between dietary fiber and salt requirements of the growing chickens (Slinger _et_ _al_., 1950). Using low fiber-high energy diets maximum growth was obtained with 0.25% or less of added salt. As the low fiber-high energy grains were replaced by high fiber-low energy grains, wheat by-products and cellulose, the salt requirement increased progressively to at least 2.0%. Unfortunately, it was not clear what grains were used in the experiment to represent the high fiber-low energy grains. Although the evidence was strong, there was no explanation for the increased requirement of salt when the chickens were fed high fiber diets.

A study relevant to the effects of fiber on the salt excretion of birds was conducted by Koike _et_ _al_. (1964). The influence of dietary fiber on route of sodium and water excretion was determined using colostomized roosters and the movement of sodium and water across the gut wall was followed in perfusion experiments. When diets low in indigestible residue were fed, sodium excretion was predominantly via urine. However, with a diet high in indigestible residue sodium was excreted mainly via feces. Urinary water was little affected, but fecal water output increased as diet residue increased. _In_ _vivo_ perfusion studies indicated that sodium efflux depended on lumen sodium concentration, while influx was constant and independent of lumen sodium concentration. Water moved readily in response to osmotic gradients. The intravenous infusion of vasopresssin caused a significant increase in net sodium movement. Unfortunately, these researchers did not adequately describe the type of the indigestible residues used in the experiment. The water solubility characteristics of the indigestible residues used in this experiment would have been of interest, because the indigestible residues largely consist of two distinctively different types, i.e., water-soluble residues and water-insoluble ones as discussed above in relation to rye and barley. Furthermore, if it is true that sodium is excreted mainly in urine in colostomized chickens fed diets low in indigestible residue, and via feces with a high residue diet, it would be of interest to know whether sodium deficiency would occur in intact chickens fed diets containing marginally low levels of sodium but rich in indigestible residue. The reasoning for this is that, unlike the sodium present in urine, most of the sodium present in feces did not have a chance to be absorbed and metabolized in the body. In other words, from a nutritional standpoint, any increase in fecal sodium represents a decrease in sodium available for utilization within the body.

It appears that the dietary fiber increases the sodium requirement of the chicken by shifting the major route of sodium excretion from urine to feces. This shift indicates that the sodium absorption in the gut is decreased by the presence of dietary fiber in the digesta. The role played by dietary fiber in reducing sodium absorption in the gut remains to be elucidated.

Experimental objectives

The purposes of the experiments reported herein were to test a hypothesis that there is a difference in water and/or electrolyte metabolism between rye-fed birds and corn-fed controls. Since the above hypothesis was proven correct through a preliminary experiment (Experiment 1), an in depth study of water and electrolyte metabolism was carried out with intact and colostomized roosters (Experiment 2). Data from Experiment 2 indicated that rye-fed birds are more vulnerable to salt, sodium in particular, deficiency. Therefore, an attempt was made to reexamine the optimum level of dietary salt for growing chickens fed rye diets in Experiment 3.

Experiment 1

A Preliminary Water Metabolism Study with Colostomized Roosters Fed Diets Based on Rye or Water-extracted Rye

INTRODUCTION

A review of the literature on the nutritional quality of rye for poultry indicates that rye has never been considered favorably as a dietary grain for poultry. One of the consistent problems associated with feeding rye to poultry is the production of wet and extremely sticky droppings (Halpin et al., 1936a; Moran et al., 1970). This condition not only causes defaecation problems but also leads to wet litter. Unlike the "wet dropping" condition which seems to be psychogenic in origin (Osbaldiston, 1969; Lintern-Moore, 1972), the sticky and/or watery droppings from birds fed rye-based diets appears to be dietary in origin. In fact, several workers (Fernandez et al., 1973b; Misir and Marquardt, 1978b) improved the excreta condition by simply extracting rye with water. Furthermore the addition of a dried water extract from rye to a corn-based diet caused the sticky excreta condition (Fernandez et al., 1973b). It appears that rye contains water-soluble substances which affect the water metabolism of the chicken.

The present experiment was designed to test the hypothesis that there is a difference in water metabolism between rye-fed roosters and corn-fed controls. Water-extracted rye was also included in this experiment to determine the influence of the water extraction process on water metabolism of the chicken. The experimental birds were surgically modified by colostomy to facilitate separate collection of urine and feces.

MATERIALS AND METHODS

Experimental birds and management. Twelve Single Comb White Leghorn (SCWL) adult roosters (Shaver strain) weighing 1.7±0.02 kg ($\overline{X}$ ± S.E.) were used in Experiment 1. The roosters were housed in individual wire-floor cages (50x45x45 cm) and experimental diets and tap water were provided *ad libitum*. The evaporation from water troughs was monitored by having a control water trough in the room. The environmental temperature was kept constant at ≈20°C. A constant lighting scheme was used throughout this study. Following acclimation to the cage environment and new diets, which normally took several days, a colostomy operation was performed on each bird and several days were allowed for recovery from the operation. Recovery was indicated by resumption of a normal feed intake, which two of the 12 birds operated on did not achieve.

Experimental diets and design. Three dietary treatments (corn, rye and water-extracted rye) were used in Experiment 1 (Table 1). The corn diet was included as a control and water extraction of rye was performed to determine the influence of the water extraction process of rye on water metabolism of the chicken. Salt was added at 0.4% level in all diets and antibiotics (100 ppm) were added to reduce microbial activity in the gut. All diets were pelleted to prevent beak impaction. One-way analysis of variance and the comparisons of treatment means by the Student-Newman-Keul's multiple range test were done as outlined by Snedecor and Cochran (1967). The limit of probability accepted as being significant was $P \leq 0.05$ for this study.

Water extraction of rye. Water-extracted rye was prepared by combining ground rye with distilled water in the proportion of 1:5 by weight

Table 1. Composition of diets used in Experiment 1

	Diets		
Ingredients	Corn	Rye	Water-extracted rye
	%	%	%
Corn	87.8	-	-
Rye (puma)	-	85.8	-
Water-extracted rye	-	-	85.8
Soybean meal (44%)	10.0	10.0	10.0
Soybean oil	-	2.0	2.0
Salt (iodinated)	0.4	0.4	0.4
Biophos[1]	1.8	1.8	1.8
Pro-strep '20' (100 ppm)[2]	+	+	+
	100.0	100.0	100.0

[1] Ca - 18%, P - 21%.

[2] Mixture of procaine penicillin (25 ppm) and streptomycin (75 ppm).

with constant stirring for 20 min. The rye suspension was centrifuged at 8,000 rpm for 10 min in a Sorvall Superspeed RC2-B centrifuge after the mixture had been allowed to stand overnight at 4°C. The residue was dried to constant weight in a draft oven at 70°C and ground (to pass a 1 mm screen) in a Wiley mill prior to incorporation into the diet. The supernatant was freeze-dried to give a water extract of rye (rye extract) for use in a later experiment. The recoveries of water-extracted rye and rye extract as a percentage of the original ground rye were 78±1.9 and 14±0.7% ($\overline{X}$ ± S.E.), respectively.

Colostomy technique. A modification of the technique of Paulson (1969) was used for the colostomy operation. Roosters were anaesthetized by administering sodium pentobarbital via a wing vein. Feathers were removed from around the cloacal orifice and the adjacent abdominal area. A circular area of skin (centered on midline), 3 cm in diameter and 2 cm anterior to the cloacal orifice, was removed from the anesthetized bird secured to an operating table. An incision, 2 cm long, was made perpendicular to the midline and in the center of the excised skin area. The cloaca was ligated with a silk suture approximately 1 cm anterior to the rectal sphincter. The rectum was then severed 0.5 cm anterior to the ligature. The severed end of the rectum was brought gently through the incision, over the exposed muscle tissue, and fastened directly to the skin by 12 to 16 evenly spaced silk sutures. A section of rigid polyethylene tubing (length, 2 cm; ID, 2 cm; wall thickness, 2 mm) was fastened around the cloacal orifice by 8 to 10 silk sutures. This tubing served as the attachment for the urine-collecting bottle.

Collection of urine and feces. Throughout this paper, the term excreta will designate the mixture of feces and urine, voided from the cloacal orifice of normal birds, whereas feces will refer to the material free of urine voided from the exteriorized colon by colostomized birds. Following the recovery from the colostomy operation, feces and urine were collected separately for 8 hours each day (9:00 a.m. - 5:00 p.m.) for 3 consecutive days. Feces were allowed to drop on the stainless steel trays placed underneath the cages; however, collections at 30 min intervals were done to minimize the moisture evaporation from the newly voided feces. Fecal samples were stored in aluminum moisture dishes with closely fitting slip-over covers. A 125 ml polyethylene bottle was connected to the polyethylene tubing by a short section of drainage tubing (Penrose Drainage Tubing, Latex, 1.9 cm diameter, Davol Rubber Co., Providence, R.I.) for urine collection. The fecal moisture was determined by drying (70°C) in a draft oven for 24 hours. Urine osmolality was measured by a freezing point depression osmometer (Model 31-LAS, Advanced Instrument Ltd.).

RESULTS AND DISCUSSION

Data obtained with regard to the water metabolism of colostomized roosters are shown in Table 2. Roosters fed a rye diet consumed significantly more water than did birds fed corn or water-extracted rye diets even though there were no differences in feed consumption among the three dietary regimes. This trend was consistent whether the water intake data were expressed per unit of body weight or per unit of feed intake. In addition, the rye diet caused the birds to excrete feces

Table 2. Water metabolism of colostomized roosters fed rye and water-extracted rye diets in Experiment 1[1]

Diet treatments[2]	Body weight (B.W.)[3] (kg)	Feed intake (F.I.)[3] (g/day)	Water intake			Fecal moisture (%)	Urine volume (g/8 hrs)	Urine osmolality (mosm/ℓ H_2O)
			(g/day)	(g/100 g F.I.)	(g/kg B.W. /day)			
Corn diet (3)	1.74 ±.012	82.2 ±10.20	203^b ±18.3	253^b ±19.2	117^b ±10.21	76.9^b ±.54	47.5^b ±4.86	401^a ±17.4
Rye diet (3)	1.69 ±.049	80.4 ±3.57	558^a ±53.8	678^a ±60.7	333^a ±21.3	83.7^a ±.41	257^a ±48.7	77^b ±10.6
Water-extracted rye diet (4)	1.65 ±.041	63.7 ±7.86	259^b ±47.5	440^b ±84.7	158^b ±31.4	76.5^b ±.27	84.4^b ±23.1	197^b ±74.7

[1] $\bar{X}$ ± S.E. (Means within a column with a common superscript are not significantly different at 5% level).

[2] Numbers within parentheses refer to the number of roosters used.

[3] No statistical analysis was done on this column.

significantly higher in moisture content than did the corn diet. This characteristic associated with rye disappeared when the grain was extracted with water, indicating a relationship between fecal moisture content and water-soluble substances present in rye.

Rye-fed roosters excreted a significantly larger volume of urine than did roosters fed the other diets. In addition, the urine from the rye-fed birds was very dilute (77±10.6 mosm/ℓ H_2O) indicating that diuretic symptoms had developed in these birds. In contrast, corn-fed birds excreted a concentrated urine (401±17.4 mosm) which was hypertonic to plasma, if the normal osmolality of the latter is assumed to be about 320 mosm (Skadhauge and Schmidt-Nielsen, 1967a; Mongin *et al.*, 1976). The water intake and urine volume values for birds fed the water-extracted rye diet tended to be intermediate to those of the rye- and corn-fed birds. Furthermore, the osmotic concentration of urine from birds fed the water-extracted rye diet was significantly lower than that from control birds (197 mosm vs. 401 mosm), indicating a mild diuresis in these birds.

It was concluded, therefore, that due to the development of diuresis normal metabolism of water in colostomized roosters was disturbed when fed a rye diet containing 0.4% added salt. The diuretic effect of rye was partially eliminated by the water extraction process. Hart and Essex (1942) reported that birds with exteriorized ureters were kept in good condition for an extended period of time by either adding 1% salt to the diet or by including salt (0.2%) in the drinking water. Apparently, the additional intake of salt was effective in preventing the development of diuresis in birds with exteriorized ureters, indicating a close relationship between water and salt metabolism.

SUMMARY

A preliminary study was carried out with 10 colostomized roosters to investigate the effect of rye and water-extracted rye on the water metabolism of the chicken. A corn diet was used as a control. The level of dietary salt was 0.4% in all diets.

Colostomized roosters fed the rye diet drank significantly more water and excreted more urine with lower osmolality than did controls. There were no differences in water consumption and urine volume between control birds and birds fed the water-extracted rye diet although values for the latter tended to be higher. The fecal moisture content was higher in rye-fed birds than in control birds or birds fed the water-extracted rye diet. Data of water intake, urine volume and urine osmolality led to the conclusion that a severe diuresis developed in birds fed the rye diet. The data also indicated that a mild diuresis may have developed in some of the birds fed the water-extracted rye diet.

Experiment 2

Influences of Diets Based on Rye or Rye Components and Dietary Salt Level on Water and Electrolyte Metabolism in Intact and Colostomized Roosters

INTRODUCTION

It was demonstrated by the results of Experiment 1 that water metabolism is altered in colostomized birds fed a rye diet. It appears that rye-fed birds are more vulnerable to diuresis than are corn-fed birds. In addition, colostomized birds are more susceptible to diuresis than are intact birds because of the separation of the urinary and alimentary tracts. As reported by Hart and Essex (1942), birds with exteriorized ureters needed more salt than did intact birds to prevent diuresis. Undoubtedly, the metabolism of water is closely associated with that of salt. When water-extracted rye was substituted for rye, it affected water metabolism in a different manner from that noted for non-extracted rye.

Experiment 2 was designed to study water and electrolyte metabolism of intact and colostomized roosters fed either a corn or rye diet supplemented with high (1.0%) and low (0.4%) salt. In addition, water-extracted rye diet and corn-based diet containing 12% rye extract, both supplemented with 1.0% dietary salt, were used in this experiment to determine the effect of water-soluble substances of rye on the water and salt metabolism of the chicken.

MATERIALS AND METHODS

Experimental birds and Management. Twenty-four SCWL roosters weighing 1.8±0.04 kg ($\overline{X}$ ± S.E.) were used in Experiment 2. Bird management and the experimental protocol were the same as described for Experiment 1 except that the roosters were placed on treatment prior to the colostomy operation and a 3-day excreta collection from the intact birds was obtained during this period. After the 3-day trial with intact roosters, a colostomy operation was performed on each bird. Separate collections of urine and feces were done for three consecutive days as described for Experiment 1, after the colostomized birds started to eat their previous experimental diets at a normal level. Feed and water were provided ad libitum. Two out of 24 birds, one from 1.0% salt-corn diet treatment and the other from 1.0% salt-water-extracted rye diet treatment, failed to recover from the operation. One colostomized rooster from 1.0% salt-water-extracted rye diet treatment remained healthy after the trial was over and it was reused in 1.0% salt-corn plus rye extract diet treatment.

Experimental diets and design. The composition of diets used in Experiment 2 is shown in Table 3. High and low levels of salt (1.0% and 0.4%, respectively) were added to corn and rye diets to determine the effect of these two levels of salt on the metabolism of water and electrolyte (Na^+, K^+ and Cl^-). In order to determine the influence of water-soluble substances present in rye, a freeze-dried water extract of rye (rye extract) was incorporated into a corn diet at a level of 12%. In addition, water-extracted rye diet containing 1.0% dietary salt was included in this experiment to determine the effect of water extraction of rye in relation to water and electrolyte metabolism of the chicken. The abbreviated forms of each dietary treatment used throughout this thesis are as follows:

1.0% C; 1.0% salt - corn diet

1.0% R; 1.0% salt - rye diet

1.0% E; 1.0% salt - corn plus rye extract diet

Table 3. Composition of diets used in Experiment 2

Ingredients	Diets[1]					
	1.0% salt-corn diet (1.0% C)	1.0% salt-rye diet (1.0% R)	1.0% salt-corn + rye extract diet (1.0% E)	1.0% salt-water-extracted rye diet (1.0% W)	0.4% salt-corn diet (0.4% C)	0.4% salt-rye diet (0.4% R)
	%	%	%	%	%	%
Corn	85.4	-	73.4	-	86.0	-
Rye (puma)	-	83.4	-	-	-	84.0
Water-extracted rye	-	-	-	83.4	-	-
Rye extract	-	-	12.0	-	-	-
Soybean meal (44%)	10.0	10.0	10.0	10.0	10.0	10.0
Soybean oil	-	2.0	-	2.0	-	2.0
Salt (iodinated)	1.0	1.0	1.0	1.0	-	0.4
Biophos[2]	1.6	1.6	1.6	1.6	0.4	1.0
Vitamin premix[3]	1.0	1.0	1.0	1.0	1.6	1.0
Mineral premix[4]	1.0	1.0	1.0	1.0	1.0	1.0
Antibiotics (100 ppm)[2]	+	+	+	+	1.0	1.0
					+	+
	100.0	100.0	100.0	100.0	100.0	100.0

[1] The analyzed Na content of each diet was as follows: 1.0% C, 0.49%; 1.0% R, 0.41%; 1.0% E, 0.47%; 1.0% W, 0.40%; 0.4% C, 0.25% and 0.4% R, 0.18%.

[2] Same as in Experiment 1.

[3] The vitamin premix provided the following per kg of diet: choline - Cl (50%), 1,500 mg; ethoxyquin, 125 mg; thiamin - HCl, 2.0 mg; riboflavin, 4.0 mg; Ca - pantothenate, 10 mg; niacin, 25 mg; pyridoxine - HCl, 3.0 mg; folacin, 0.55 mg; biotin, 0.15 mg; vitamin B_{12}, 0.01 mg; menadione - Na, 0.55 mg; vitamin A, 1,500 IU; vitamin D, 800 IU; and vitamin E, 10 IU.

[4] The mineral premix provided the following per kg of diet (mg): MnO_2, 44 mg; ZnO_2, 60 mg; $CuSO_4 \cdot 5H_2O$, 16 mg; $FeSO_4 \cdot 7H_2O$, 400 mg; and KCl, 3,000 mg.

1.0% W; 1.0% salt - water-extracted rye diet

0.4% C; 0.4% salt - corn diet

0.4% R; 0.4% salt - rye diet

Data from Experiment 2 were subjected to a one-way analysis of variance test and means were compared by the multiple range test of Student-Newman-Keul as outlined by Snedecor and Cochran (1967). The limit of probability accepted as being significant was $P \leq 0.05$.

Collection of excreta, feces and urine. Feces and urine were collected as described in Experiment 1. The collection of excreta samples was also as described for feces. At the termination of each 8-hour collection period during each day of the 3-day collection periods, aliquot mixtures of excreta or feces were centrifuged at 12,000 rpm for 10 min to obtain excreta and fecal fluids, respectively. The residues were discarded. The rest of the samples were dried at $70^{\circ}C$ for 24 hours and pooled to give one sample per bird for further analysis. In order to estimate the total 24-hour dry matter excretion by the intact birds, excreta were allowed to accumulate on the trays for an additional 16 hours (5:00 p.m. - 8:00 a.m.), and were collected and dried as described above. This value was then used to calculate the dry matter metabolizability of each diet and the total daily water excretion for each bird. Invisible water loss was assumed to be the difference between total water intake and total water excretion.

Collection and handling of blood samples. Blood samples ($\approx$8 ml/bird) were obtained from each rooster before and after colostomy operation by heart puncture technique at the termination of each collection period. Plasma samples obtained by centrifuging the blood at 3,500 rpm for 20 min at $4^{\circ}C$ were kept frozen for future analysis. Packed cell volume was determined by the microhematocrit method using an International hematocrit centrifuge (12,000 rpm for 5 min) and hematocrit reader.

Chemical analyses. Sodium and potassium concentrations in urine and plasma were determined using a Technicon Autoanalyzer II (model 7-70-140A). The chloride content of plasma and urine was measured with a chloride analyzer (Chloridometer, model IL279, Instrumentation Laboratory, Inc.). Sodium, potassium and chloride concentrations in solid materials were analyzed by atomic absorption spectrophotometry (Perkin Elmer, model 303) after extracting the samples by the method of AOAC (1975).

Calculation of plasma clearance. Plasma clearance for each electrolyte and free water clearance (C_{H_2O}) were calculated by the following formulae;

$$\text{Plasma clearance } (\mu l/min) = \frac{\text{Quantity of urine } (\mu l/min) \times \text{Electrolyte concentration in urine}}{\text{Electrolyte concentration in plasma}}$$

$$C_{H_2O}\ (\mu l/min) = \text{Urine volume } (\mu l/min) - C_{osm}\ (\mu l/min)$$

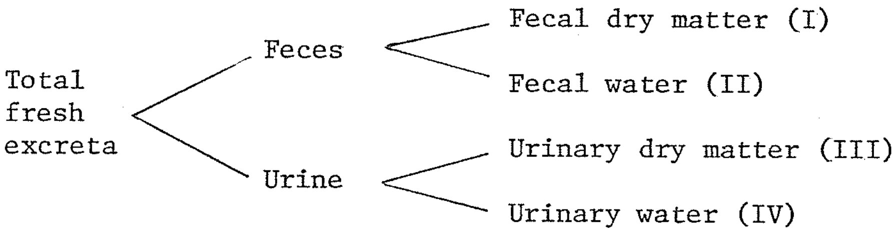
$$C_{osm}\ (\mu l/min) = \frac{\text{Osmols entering urine per min}}{\text{Plasma osmolar concentration}}$$

It was assumed in these calculations that the cloaca plays a minor role in the post renal modification of urine (Hart and Essex, 1942; Hill and Lumijarvi, 1968; Nechay and Lutherer, 1968).

Estimation of total water excretion. In estimating total water excretion (T.W.E.) by the birds, the moisture content of excreta collected for 8 hours was extrapolated to represent the moisture content of excreta collected for 24 hours. The following formula was used to calculate the T.W.E. per day:

$$\underset{(\text{g/day})}{\text{T.W.E.}} = 100 \times \frac{\text{Total D.M. of excreta (g/day)}}{\text{\% D.M. of fresh excreta}} - \text{Total D.M. of excreta (g/day)} \qquad (\text{Eq. 1})$$

Estimation of secondary urinary water excretion. Secondary urinary water excretion (U') is defined as the volume of urinary water excreted after the ureteral urine (U) has gone through the post-renal reabsorption, if any, in the cloaca and large intestine. For the purpose of comparison of urinary water excretion among the different dietary treatments, U' was calculated indirectly by the following steps:



$$\underset{(\text{II} + \text{IV})}{\text{T.W.E.}} - \underset{(\text{II})}{\text{F.W.E.}} = \underset{(\text{IV})}{\text{U}'} \qquad (\text{Eq. 2})$$

$$\underset{(\text{II})}{\text{F.W.E.}} = 100 \times \frac{\text{T.D.M.E. (I + III)}}{\text{\% D.M. F.}} - \underset{(\text{I} + \text{III})}{\text{T.D.M.E.}} \qquad (\text{Eq. 3})$$

where:

T.W.E. = total water excretion (g/day) = II + IV

F.W.E. = fecal water excretion (g/day) = II

U' = secondary urinary water excretion (g/day) = IV

T.D.M.E. = total dry matter excretion (g/day) = I + III

% D.M. F. = % dry matter of fresh feces

An assumption made in the preceding calculation is that, if the excreta are not contaminated with urine, the % dry matter of that excreta is constant in the same bird fed the same diet. The % dry matter of excreta without urine was approximated by the % dry matter of fresh feces (% D.M. F.) obtained from colostomized birds. Another assumption necessary to validate the calculation is that the urinary dry matter excretion (III) is negligible compared to the total fecal dry matter excretion (I). Since the urinary dry matter excretion is larger than zero under any condition, the latter assumption obviously tends to overestimate the value of F.W.E. and, consequently, underestimate the U'. It is postulated, however, that the degree of error incurred by this assumption would be similar among treatments, making comparisons among U' values possible.

Measurement of viscosity. A viscometric method using an Ostwald-type viscometer developed by Tipples (1969) was used to measure the viscosities of diet extracts and fluids of excreta and feces. Diet extracts were prepared by centrifuging a mixture of 1 g of finely ground diet and 9 ml of distilled water at 12,000 rpm for 10 min. For purposes of standardization, each viscometer was calibrated at 20°C against a series of 3 ml aliquots of glycerol-water solution ranging in viscosity from about 1.22 to 10.68 cP (centipoises)[1]. For each viscometer a straight-line calibration curve was obtained for viscosity against flow time. When the samples were too thick to flow down the capillary bore, which happened quite often with samples from rye treatments, dilutions were made by adding equal amounts of distilled water. All measurements were done at 20°C using 3 ml of sample.

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[1] CRC Handbook of Chemistry and Physics. 1978. 59th ed., CRC Press Inc.

Measurement of bulk density. A method for determining the bulk density of soils[2] was modified to measure the bulk density of grain and dried fecal samples. Samples were finely ground in a hammer mill to pass through a 1 mm sieve. Three grams of each sample were weighed and transferred to a graduated conical centrifuge tube (12 ml capacity). The tube was then dropped 10 times onto several thickness of paper towelling from a height of ≈5 cm to compact the contents. The volume of the sample was read and the bulk density was expressed as g (D.M.)/ml.

Measurement of water holding capacity. A method for determining the water holding capacity of soil[3] was modified to measure the water holding capacity of grains and fecal samples. Samples were ground in a hammer mill equipped with a 1 mm sieve. One gram of sample was mixed thoroughly with 4 g of sea sand (washed and ignited) to promote the spread and filtration of water into and among sample particles. Small rounds of filter paper were cut to fit in the neck of a glass funnel 10 cm in diameter and were used to prevent sample mixtures from falling out of the bottom of the funnel. The filter paper piece was saturated with distilled water and the free-water line in the funnel was marked. The mixture of sample and sea sand was then placed in the funnel in a support ring on a retort stand. The sample mixture was moistened slowly with water from a burette, drop by

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[2] Laboratory Manual for Introductory Soils. 1980. Univ. of Manitoba.

[3] Laboratory Manual for Ecological Microbiology A. 1978. Univ. of Manitoba.

drop, until the surface of the sample mixture was all moistened. More water was added, drop by drop, until the mixture was saturated completely which was noted by the first movement of the free-water line beyond its previous mark. The water holding capacity of pure sand was determined and subtracted from the total measured volume.

RESULTS AND DISCUSSION

I. Water Metabolism of Intact and Colostomized Roosters Fed Experimental Diets

A. Water metabolism of intact roosters

Data on water metabolism of intact roosters from Experiment 2 are summarized in Table 4. When 1.0% salt was added to diets, there were no differences in water consumption among the 1.0% salt dietary treatments except between 1.0% R and 1.0% W. Roosters fed the 1.0% W diet consumed significantly less water than did birds fed the 1.0% R diet when compared on either a body weight basis or a feed intake basis. In general, birds fed the 1.0% W diet seemed to drink less water than did birds fed the other diets containing 1.0% salt. When 0.4% salt was added to diets, a significant difference was found between birds fed the corn and rye diets. In this case, birds fed the 0.4% R diet drank more water than did birds fed the 0.4% C diet.

When the salt level was decreased from 1.0% to 0.4%, the corn-fed birds decreased water consumption. However, the rye-fed birds did not change water consumption in response to the change in the level of dietary salt. These data appear to be a definite contradiction to the findings of Kare and Biely (1948) who reported that the addition of increasing

Table 4. Influence of experimental diets on water metabolism of intact roosters[1]

Diet treatment[2]	Body weight (B.W.)[3] (kg)	Feed intake (F.I.)[3] (g/day)	Water intake			Excreta moisture (%)	Total water excretion		Invisible water loss[4]	
			(g/day)	(g/100 g F.I.)	(g/kg B.W. /day)		(g/day)	(g/kg B.W. /day	(g/day)	(g/kg B.W. /day)
1.0% C	2.07 ±.060	84.2 ±5.60	250^{ab} ±17.4	298^{ab} ±12.4	120^{ab} ±4.8	87.6^{a} ±.27	155^{abc} ±11.3	74.8^{bc} ±3.41	99.7 ±7.07	48.1 ±2.00
1.0% R	2.07 ±.085	83.7 ±8.68	290^{a} ±38.3	352^{a} ±35.1	140^{a} ±18.1	87.2^{a} ±.29	191^{a} ±20.0	92.5^{ab} ±9.81	103.7 ±21.13	49.9 ±9.90
1.0% E	1.70 ±.037	70.1 ±5.63	211^{ab} ±16.2	302^{ab} ±11.0	124^{ab} ±9.9	87.0^{a} ±.22	130^{bcd} ±15.3	76.3^{bc} ±8.60	85.9 ±14.03	51.0 ±9.12
1.0% W	1.75 ±.071	77.0 ±0.92	181^{b} ±8.7	236^{bc} ±11.8	104^{bc} ±8.0	84.3^{b} ±.76	112^{cd} ±5.9	64.4^{c} ±3.87	73.0 ±5.42	42.3 ±4.77
0.4% C	1.75 ±.040	75.8 ±1.30	167^{b} ±8.9	220^{c} ±10.9	95^{c} ±5.2	83.8^{b} ±.42	101^{d} ±4.8	58.0^{c} ±3.53	71.1 ±12.70	40.4 ±7.13
0.4% R	1.69 ±.029	73.5 ±3.43	233^{ab} ±11.0	321^{ab} ±25.2	139^{a} ±8.0	87.3^{a} ±.26	174^{ab} ±8.7	103.6^{a} ±6.51	61.4 ±5.03	36.5 ±3.26

[1] $\overline{X}$ ± S.E. (Means within a column with a common or no superscript are not significantly different at 5% level).

[2] Four roosters were used per treatment. For full description refer to Materials and Methods (page 50-52).

[3] No statistical analysis was done on this column.

[4] Invisible water loss = water intake (drinking water and feed moisture) - total water excretion.

amounts of salt to a diet caused a progressive increase in water intake per gram of feed. In addition a high positive correlation was observed by Kondo and Ross (1962a, b) between the amount of sodium and/or potassium in the feed, and the water consumption in the growing chicken. The excreta moisture content was also positively correlated to dietary sodium and potassium content. It appears, therefore, that the linear relationship between dietary salt level and water intake can be affected, to a limited degree, by the type of diet being fed.

The moisture content of excreta from birds fed the 1.0% W diet was significantly lower than those from birds fed the 1.0% C, 1.0% R or 1.0% E diets. There were no differences, however, in excreta moisture content among the latter three groups. Fernandez et al. (1973b) reported that excreta condition was significantly improved by the water extraction process of rye and that a dried water extract of rye caused a sticky excreta condition when added to a corn diet. Similar observations were made by Misir and Marquardt (1978b). The reduction of excreta moisture content of rye-fed birds by the water extraction process as shown in Table 4 appears to be due to the elimination of water-soluble substance(s), which have hydrocolloidal properties, from rye.

When a low level of salt (0.4%) was added to the diets, birds fed the corn diet excreted less watery excreta than did birds fed the rye diet. This was consistent with the observation of Moran et al. (1970) who reported that rye could comprise up to 25% of the grain component without adverse effects when compared to birds fed the control diet based on corn even though the litter moisture was significantly increased. When the level of dietary salt was increased from 0.4% to 1.0%, the difference in moisture content of excreta between birds fed corn and rye diets disappeared apparently due to the excessive salt intake on the part of birds fed corn diets. This excessive salt intake might have forced the birds to drink more, and concomitantly to excrete more water as shown in Table 4. According to Kondo and Ross (1962b), the addition of graded levels of salt to chicken diets resulted in increased excreta moisture with each increment of salt. Hurwitz et al. (1973) also found a positive dependence of excreta moisture on total dietary sodium and on the Na/Cl ratio. While roosters fed corn diets increased excreta moisture content significantly as the salt level increased, birds fed rye diets did not respond in this respect to the change in dietary salt level. In addition, birds fed rye diets showed no difference in water intake or total excretion of water per day between the two levels of dietary salt used in this experiment. In other words, the addition of 1% salt to the rye diet was not enough to cause birds to drink more, to excrete droppings of a more watery consistency or to excrete more water than did birds on a rye diet containing 0.4% added salt. This result indicates that birds fed diets based on rye are more resistant to excessive intake of salt than are birds fed diets based on corn.

The pattern of total water excretion generally follows the same trend as that of water intake. When 1.0% salt was added to diets, there were no differences in total water excretion among treatments except between 1.0% R and 1.0% W. Roosters fed the 1.0% W diet excreted significantly less water than did birds on the 1.0% R diet reflecting the influence of the water extraction process of rye on water metabolism in the chicken. Birds fed the 0.4% C diet excreted significantly less water than did birds on the 0.4% R diet regardless of whether the data were expressed per unit of body weight basis or per bird basis. Corn-fed birds tended to excrete more water as the salt level increased from 0.4% to 1.0%. However, rye-fed birds excreted a similar amount of water regardless of the dietary salt level.

The invisible water loss, probably mainly due to evaporation from the lungs, ranged from 60 g to 104 g per day per bird. If the metabolic water produced in the body was taken into consideration, the values would have been considerably higher. Hart and Essex (1942) estimated the water loss from respiration ranging from 110 to 144 g per day per hen. However, Medway and Kare (1959) reported that the mean water loss due to evaporation from the lungs in 32-week old hens (≃2 kg in body weight) was 53 g per day. There were no significant differences in invisible water loss among the dietary treatments employed in Experiment 2.

As discussed above, roosters fed a diet based on water-extracted rye appeared to drink less and excrete less water than did birds fed diets based on rye. Also birds fed water-extracted rye excreted excreta of a less watery consistency than did birds fed rye. These differences between the water-extracted rye and non-extracted rye could be attributed to the elimination of water-soluble substances, which have hydrocolloidal properties, from rye by the water extraction process. The addition of the rye extract to a corn diet at a level of 12%, however, had no effect on water metabolism of the intact roosters. No explanation is available for this apparent contradiction.

When 0.4% salt was added to diets, birds fed the corn diet drank less, excreted droppings of a less watery consistency and less total water than did birds on a rye diet. When the dietary level of salt was increased from 0.4% to 1.0%, birds fed a corn diet increased water consumption and water excretion, indicating an enhanced water turn-over rate due to the over-consumption of salt. The results also indicated that birds fed rye diets were more resistant to excessive intakes of salt than were corn-fed birds since the rye-fed birds did not change water metabolism even though the dietary salt level was increased from 0.4% to 1.0%.

B. Water intake and fecal moisture content of colostomized roosters

The response to dietary treatment in water intake was different between colostomized and intact roosters. As shown in Table 5, no significant differences were found in water intake among colostomized roosters fed the six different diets. A high degree of variability existed within treatments, especially in 0.4% R. Although statistically not significant, colostomized birds fed corn diets tended to increase water consumption as the dietary salt level increased from 0.4% to 1.0%. As discussed above, this was also true for intact roosters. On the other hand, colostomized birds fed rye diets tended to decrease water consumption as the dietary salt level increased from 0.4% to 1.0%. This reverse trend was due mainly to the development of diuresis in some of the birds fed the 0.4% R diet, causing great variations in water intake data for that treatment. Two out of four colostomized birds fed the 0.4% R diet developed diuresis. One of these birds developed a mild case of diuresis excreting urine slightly hypotonic to plasma (270±4.0 mosm/ℓ H_2O) while the other showed a severe case (117±21.0 mosm/ℓ H_2O). In addition to the rye diet containing 0.4% dietary salt, the water-extracted rye diet

Table 5. Water intake and fecal moisture content of colostomized roosters fed experimental diets[1]

Diet treatments[2,3]		Body weight (B.W.)[4] (kg)	Feed intake (F.I.)[4] (g/day)	Water intake (g/day)	Water intake (g/100 g F.I.)	Water intake (g/kg B.W./day)	Fecal moisture content (%)
1.0% C	(3)	1.91 ±.180	75.2 ±3.64	277 ±19.6	369 ±8.9	146 ±4.4	77.7^{c} ±.51
1.0% R	(4)	2.00 ±.096	75.0 ±3.25	295 ±27.7	392 ±22.4	147 ±12.4	84.5^{a} ±.32
1.0% E	(5)	1.68 ±.063	63.7 ±6.34	232 ±20.9	369 ±14.1	138 ±11.4	80.3^{b} ±.98
1.0% W	(3)	1.69 ±.098	64.8 ±7.32	281 ±23.2	468 ±103.3	170 ±24.0	80.5^{b} ±.68
0.4% C	(4)	1.67 ±.057	61.2 ±6.54	179 ±15.4	294 ±17.4	107 ±6.6	78.0^{c} ±.54
0.4% R	(4)	1.56 ±.108	74.5 ±2.39	362 ±83.5	488 ±118.6	245 ±76.7	82.6^{ab} ±.43

[1] $\overline{X}$ ± S.E. (Means within a column with a common or no superscript are not significantly different at 5% level).

[2] Numbers within parentheses refer to the number of roosters used for each treatment.

[3] For full description refer to Materials and Methods (page 50-52).

[4] No statistical analysis was done on this column.

also caused diuresis in two out of three colostomized birds even though this diet contained 1.0% added salt.

The development of diuresis in some of the birds fed the 0.4% R diet in this experiment was in agreement with the result from Experiment 1, where all three colostomized birds fed a rye diet containing 0.4% dietary salt developed diuresis. It is interesting to note that the diuresis could be prevented by simply increasing the salt level from 0.4% to 1.0% in diets based on rye. A similar result was reported by Hart and Essex (1942) although these researchers did not identify the symptoms in their operated hens as diuresis. The apparent cause of diuresis observed in this study was a salt deficiency in the body, which in turn affected water metabolism. In the development of diuresis water consumption increases followed by increased urine excretion in an attempt to maintain homeostasis. In this experiment, water intake of diuretic birds ranged from 500 to 820 g per 100 g feed intake.

The process of water extraction of rye caused some changes in water metabolism of colostomized roosters. Unlike intact roosters fed the 1.0% W diet, colostomized birds fed the same diet did not drink less water than did colostomized roosters fed the 1.0% R diet. This might be explained, as mentioned above, by the fact that two out of three colostomized birds on the 1.0% W diet developed mild diuresis, excreting urines slightly hypotonic (183-288 mosm) to plasma.

A markedly different physical constituency and pattern of response to dietary treatment with regard to moisture content was observed for feces from colostomized roosters as compared with excreta obtained from intact roosters. Unlike the watery, unformed excreta, all of the feces were firm, dry and well-formed, obviously due to the prevention of feces from being mixed with ureteral urine. The dietary salt level did not affect the fecal moisture content significantly in birds fed either corn or rye diets. Feces from birds fed rye diets were significantly higher in moisture content than were those from birds fed corn diets regardless of dietary salt level. The 1.0% E and 1.0% W treatments gave intermediate results. It appears that feces from rye-fed birds inherently contain substances that increase fecal moisture. The water extraction process of rye was partially successful in removing these substances. When the freeze-dried rye extract was added to a corn diet at a level of 12% and fed to colostomized roosters, it increased the fecal moisture content significantly, but not to the same degree as for rye, per se.

C. Comparison of water intake of roosters before and after colostomy

Comparisons were made of water intake of roosters before and after the colostomy operation as shown in Table 6. When water intake data were expressed per unit of feed intake, the colostomized roosters drank significantly more water than did intact birds except the birds fed rye diets. The diuretic symptoms developed in some of the colostomized birds fed the 1.0% W and 0.4% R diets caused a high degree of variation within treatments as discussed above thereby reducing the chance of detecting significant difference especially in the 0.4% R treatment. When a paired t-test was conducted between intact and colostomized roosters utilizing the mean values for each treatment as replicates, it was found out that the colostomized birds drank significantly more water per unit of feed intake than did intact birds. A similar

Table 6. Comparison of water intake of roosters before and after the colostomy operation[1,2]

	Water intake (g/100 g F.I.)			Water intake (g/day/kg B.W.)		
Diet treatments[3]	Before colostomy	After colostomy	t-test	Before colostomy	After colostomy	t-test
1.0% C	298±12.4	369±8.9	$P \leq 0.01$	120±4.8	146±4.4	$P \leq 0.05$
1.0% R	352±35.1	392±22.4	N.S.	140±18.1	147±12.4	N.S.
1.0% E	302±11.0	369±14.1	$P \leq 0.01$	124±9.9	138±11.4	N.S.
1.0% W	236±11.8	468±103.3	$P \leq 0.05$	104±8.0	170±24.0	$P \leq 0.05$
0.4% C	220±10.9	294±17.4	$P \leq 0.05$	95±5.2	107±6.6	N.S.
0.4% R	321±25.2	488±118.6	N.S.	139±8.0	245±76.7	N.S.
Overall mean	288±20.7	397±29.2	$P \leq 0.05$[4]	120±7.4	159±19.1	$P \leq 0.10$[4]

[1] $\bar{X}$ ± S.E.

[2] N.S. refers to non-significant.

[3] For full description refer to Materials and Methods (page 50-52).

[4] Paired t-test.

trend was also found when the water intake data were expressed per unit of body weight although the degree of significance decreased to 10% level. These results are consistent with the findings of Dicker and Haslam (1966) who reported that adult roosters increased the ratio of water to feed intake considerably after the ureters were exteriorized. The difference between the amounts of water drunk by operated and non-operated birds was taken by these workers as a measure of the amount of water normally reabsorbed by the post-renal reabsorption of urinary water in the cloaca and colon. Lumijarvi _et_ _al_. (1967) reported a marked increase in water intake and urine excretion in colostomized hens fed a diet lacking in sodium, potassium and chloride. Intact hens under similar conditions showed a smaller increase than did operated hens in this respect. When these electrolytes were adequately supplied in the diet, water intake and excretion were quite similar in intact and colostomized hens. Although the colostomy operation tended to increase the water intake in the current experiment, it appears that the influence of colostomy on the water consumption is subject to variations depending on the type of diet and on dietary electrolyte concentrations. This is indicated by the fact that the effect was not consistent among dietary treatments.

D. Pattern of water excretion in intact roosters

An attempt was made to differentiate the routes of water excretion in intact roosters. As shown in Table 7, there were no significant differences in total water excretion (T.W.E.) among 1.0% salt treatments except between the 1.0% R and 1.0% W treatments, reflecting the influence

Table 7. Pattern of water excretion in intact roosters fed experimental diets[1]

Diet treatments[2]	Total water excretion (T.W.E.) (g/kg/day)	Fecal water excretion (F.W.E.) (g/kg/day)	Secondary urinary water excretion (U') (g/kg/day)
1.0% C	74.8 ± 3.41^{bc}	35.5 ± 1.57^{b}	39.2 ± 2.01^{a}
1.0% R	92.5 ± 9.81^{ab}	72.8 ± 8.49^{a}	19.8 ± 2.98^{c}
1.0% E	76.3 ± 8.60^{bc}	49.4 ± 8.11^{b}	27.0 ± 1.95^{b}
1.0% W	64.4 ± 3.87^{c}	47.9 ± 3.40^{b}	16.5 ± 1.65^{c}
0.4% C	58.0 ± 3.53^{c}	39.4 ± 2.06^{b}	18.6 ± 2.25^{c}
0.4% R	103.6 ± 6.51^{a}	70.4 ± 4.55^{a}	33.2 ± 2.35^{ab}

[1] $\bar{X}$ ± S.E. (Means within a column with a common superscript are not significantly different at 5% level).

[2] For full description refer to Materials and Methods (page 50-52).

of the water extraction process of rye. However, the rye extract added to a corn diet did not have an influence on water excretion. Corn-fed roosters, in general, excreted less water than did rye-fed birds at both salt levels.

In terms of fecal water excretion (F.W.E.), the corn-fed birds excreted significantly less fecal water than did rye-fed birds regardless of dietary salt level. In addition, birds fed the 1.0% W diet excreted significantly less water than did birds fed the 1.0% R diet, reflecting the influence of the water extraction process of rye on F.W.E. The rye extract, however, did not affect F.W.E. significantly when added to a corn diet at a level of 12%. As discussed above, the equation used in this calculation tended to overestimate the amount of F.W.E. by neglecting urinary dry matter excretion.

Secondary urinary water excretion (U') was assumed to be the difference between T.W.E. and F.W.E. The U' values tended to be underestimated because of the overestimation of F.W.E. However, it was postulated that the size of error incurred by this over- and/or underestimation of F.W.E. and U', respectively, would be consistent among treatments. The birds fed the 1.0% C diet excreted significantly higher U' than did birds fed 1.0% R, 1.0% E or 1.0% W diets. There was no significant difference between 1.0% R and 1.0% W treatments. This result indicates that the water-extraction process of rye did not affect U' significantly. The addition of the rye extract to a corn-diet containing 1.0% dietary salt decreased U' significantly. When the salt level was increased from 0.4% to 1.0%, corn-fed birds increased U' significantly. In the case of rye-fed birds, however, U' decreased significantly as the dietary salt level increased from 0.4% to 1.0%. This result indicates that the excreta moisture content of intact birds fed rye may be decreased, albeit to a limited degree, by simply increasing the dietary salt level. The possibility of doing so would increase for diets marginally low in salt since the chance of developing diuresis also increases. Further research is needed to test the feasibility of reducing the excreta moisture in intact birds by increasing the dietary salt level. In this experiment, however, no significant improvement was made when the dietary salt level was increased from 0.4% to 1.0% among rye-fed birds.

E. Osmotic concentrations of plasma, urine and excreta and fecal fluids of roosters

Data of osmotic concentrations of plasma, urine and excreta and fecal fluids of roosters fed the various experimental diets are summarized in Table 8. No significant differences were found in plasma osmolality among the diet treatments before or after the colostomy operation. Pang _et al_. (1978) reported that poults on a low sodium diet (0.005% Na) showed significantly lower osmolal concentrations than did poults fed a control diet. However, Harris and Koike (1977) found no difference in plasma osmolality between pullets fed a sodium restricted diet (0.017% Na) and a control diet (0.2% Na). The absence of response to different dietary salt levels in plasma osmolality in this experiment might be explained by the fact that the 0.4% dietary salt level might not have been low enough to decrease the plasma osmolality in adult roosters. A significant difference was detected in plasma osmolality when a paired t-test was conducted between intact and

Table 8. Osmotic concentrations of plasma, urine and excreta and fecal fluids of roosters fed experimental diets[1]

	mosm/ℓ H_2O				
	Plasma[3]				
Diet treatments[2]	Intact roosters	Colostomized roosters	Fecal fluid from colostomized roosters	Excreta fluid from intact roosters	Urine from colostomized roosters
1.0% C	322±4.4	311±1.5	373±7.1^{ab}	490±10.7^{a}	505±48.2^{a}
1.0% R	316±9.0	310±3.6	388±12.8^{a}	449±21.3^{ab}	541±37.2^{a}
1.0% E	319±2.5	308±3.3	391±11.4^{a}	425±29.1^{ab}	455±21.2^{ab}
1.0% W	319±3.9	307±2.6	345±3.8^{b}	385±26.9^{ab}	274±48.8^{b}
0.4% C	309±1.9	309±1.9	389±8.7^{a}	431±47.1^{ab}	518±20.4^{a}
0.4% R	309±1.8	309±1.8	415±7.2^{a}	359±14.2^{b}	338±92.0^{ab}

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[1] $\overline{X}$ ± S.E. (Means within a column with a common or no superscript are not significantly different at 5% level).

[2] For full description refer to Materials and Methods (page 50-52).

[3] The plasma osmolality of intact roosters (316±2.2) was significantly higher ($P \leq 0.05$) than that of colostomized birds (309±0.6) when paired t-test was conducted between intact and colostomized birds.

colostomized roosters utilizing the mean values for each treatment as replicates. The plasma osmolality of the former was significantly higher than that of the latter, indicating the influence of the colostomy operation in this respect.

There was no trend in the osmolality of fecal fluids except that the value for the 1.0% W treatment was lower than those for all other treatments. As with the other parameters studied, these data indicate that the water extraction process of rye has an influence on water metabolism of the chicken. Interestingly the fecal fluid was hypertonic to plasma, indicating that the absorption of water occurred against a concentration gradient in the gut. This result is in agreement with the findings of Mongin _et al_. (1976) who reported that the absorption of water across the proximal jejunum was achieved against a gradient of about 330-420 mosm in the fowl. These same workers also reported that the osmolality of the contents of proximal and distal ileum of the hen were 514 and 451 mosm/ℓ H_2O, respectively, which is similar to the values of fresh excreta fluid obtained in this experiment with minor exceptions.

As discussed above, diuresis had developed in two out of three birds fed the 1.0% W diet and two out of four birds fed the 0.4% R diet. The osmotic concentrations of urine collected from these diuretic birds were lower (110-290 mosm/ℓ H_2O) than those from normal birds (350-538 mosm), decreasing the mean urinary osmolality values of these treatments as shown in Table 8. Since urine which varies in osmolality and ionic concentration flows back into the coprodeum and the colon and even into the cloaca, modification of the composition of the contents of these segments of the gastrointestinal tract and, therefore, of the milieu of the mucosal side of the epithelial cells would be expected (Koike and McFarland, 1966; Akester et al., 1967; Skadhauge, 1968). According to Skadhauge (1968), the average osmolality of the contents of the cloaca ranged from 489 to 143 mosm in the dehydrated and hydrated states, respectively, and in the colon from 376 to 192 mosm.

It is of interest to note from the data presented in Table 8 that, with one exception, the osmolality values of excreta fluid tended to fall in between those of fecal fluid and urine. The intermixing of the digesta of the colon and the cloaca with urine would account for this phenomenon. The exception to this is the excreta fluid from birds fed the 1.0% W diet, which tended to have a higher osmolality than either fecal fluid or urine. A possible explanation for this anomaly might be that a significant portion of ureteral water was absorbed in intact birds fed the 1.0% W diet. The urine from the birds fed the 1.0% W diet showed remarkably low osmolality indicating that diuresis had developed in some of these birds. Another interesting fact in this regard is that the osmolality of excreta fluid tended to be lower than that of fecal fluid in birds fed the 0.4% R diet. This would be taken as indirect evidence that intact birds fed the 0.4% R diet excreted a dilute urine possibly due to the development of diuresis. The development of diuresis, however, would not be noticed in the intact birds unless separate collection and analyses of urine and feces were done. This view is supported by the fact that the intact birds fed the 0.4% R diet showed significantly higher water consumption and excretion than did birds fed the 0.4% C diet as shown in Table 4.

F. Comments on the colostomy operation and the resultant symptoms of diuresis and constipation

To study the metabolism of water and electrolyte in poultry, separate collection of urine and feces is often necessary. Although several methods have been reported for the colostomy operation to achieve this, attempts to duplicate these techniques in this laboratory were often encountered with two problems. One is the development of diuresis and the other is the recurring blockage of the artificial anus due to constipation. Hart and Essex (1942) and Paulson (1969) also reported similar problems. As indicated by Hart and Essex (1942), the problem of diuresis was successfully overcome by adding extra salt to the diets in this laboratory. Paulson (1969) reported that 5 to 10% of the birds exhibited mild diuresis following surgery.

The problem of constipation was more serious. According to Hart and Essex (1942), none of the birds that had artificial anuses remained suitable for experimentation for more than 3 weeks. These workers reported that after about 3 weeks the gut became atonic and even though the new anus was adequately patent, defecation was slow and obstruction inevitable. Paulson (1969) reported that about 5% of the operated birds displayed the recurring blockage problem and efforts to restore them to a normal physiological condition were usually unsuccessful. None of these workers, however, identified this problem as constipation. In this study, the colostomized birds were, in many cases, suitable for experimentation for only 2-3 weeks due to the development of constipation. The colon was enlarged tremendously (megacolon or Hirshsprung's disease) and the content of colon was covered with thick mucus. There was no recurring blockage of the new anus due to the regrowth of the skin. Guyton (1976) described that a frequent cause of constipation in humans is irregular bowel habits that have developed through a lifetime of inhibition of the normal defecation reflexes. Constipation can also result from spasm of a small segment of the sigmoid of colon. The cause of constipation in colostomized birds appears to be due to the disturbance of colonic motility inflicted by the colostomy operation, per se.

II. Dry Matter Metabolizability of Experimental Diets

The mean values for dry matter (DM) metabolizability of experimental diets by intact roosters are shown in Table 9. No significant differences were found in DM metabolizability between 1.0% C and 0.4% C diets, or between 1.0% R and 0.4% R diets. The DM metabolizabilities of rye diets were significantly lower than those of the other diets. When water-extracted rye was substituted for rye, the DM metabolizability of the diet was significantly improved such that it was equivalent to those of the corn diets. It can be suggested from these results that rye contains a higher level of dietary fiber than does corn or water-extracted rye. The increased DM metabolizability of rye by the water extraction process can be related to improved chicken growth and feed efficiency as reported by Fernandez _et al_. (1973b). These workers indicated that the fraction of rye that contains most of the growth depressing properties for chickens and also contains the factor causing sticky droppings in young birds can be removed by simple water extraction. It was further indicated that the sticky droppings phenomenon, per se, is not deleterious to growth of the chicken and that this effect is caused by a

Table 9. Dry matter metabolizability of experimental diets by intact roosters[1]

Diet treatments[2]	Dry matter intake (g/day)	Dry matter excretion (g/day)	Dry matter metabolizability (%)
1.0% C	79.1±5.26	21.9 ± 1.54^{b}	72.3 ± 0.80^{a}
1.0% R	78.6±8.17	27.3 ± 2.10^{a}	64.9 ± 1.68^{b}
1.0% E	66.1±5.32	19.5 ± 2.28^{b}	71.0 ± 0.84^{a}
1.0% W	72.4±0.87	20.7 ± 0.17^{b}	71.5 ± 0.15^{a}
0.4% C	70.0±1.19	19.5 ± 0.62^{b}	72.2 ± 0.85^{a}
0.4% R	67.9±3.17	24.9 ± 0.72^{ab}	64.4 ± 0.91^{b}

[1] $\overline{X}$ ± S.E. (Means within a column with a common or no superscript are not significantly different at 5% level).

[2] For full description refer to Materials and Methods (page 50-52).

factor that is different from the one that causes growth depression.

The addition of rye extract to a corn-based diet at a level of 12% did not reduce the DM metabolizability in intact roosters. According to Fernandez et al. (1973b) and Misir and Marquardt (1978b), a freeze-dried rye extract caused growth depression in young chickens. Unfortunately, it was not clarified as to why the freeze-dried rye extract resulted in growth depression.

The mechanism by which the water extraction process brings about the increased DM metabolizability of rye is not clear. The water extraction process of rye may not only fractionate the water-soluble substances, including water-soluble pentosans, from rye but also exert an effect similar to the water soaking and/or water treatment process on the water-insoluble components (i.e., water-extracted rye). According to Potter et al. (1965), the M.E. of barley increased 22% by water treatment. The increased M.E. of the barley by water treatment was attributed to the significantly increased digestibility of the protein, fat, and to a lesser degree, N.F.E. Adams and Naber (1969a, 1969b) suggested that the enhanced growth and energy utilization responses by the chicken to water treatment of ground barley or wheat could be attributed to the ability of moisture to modify the digestibility of the starch granule. It was concluded in subsequent studies (Naber and Touchburn, 1969a, 1969b) that the water treatment probably increased the susceptibility of starch to enzymatic degradation and thereby promoted increased energy utilization by the chicken. More studies are needed to investigate the interrelationships among the growth depressing properties of rye, the water extraction process and the effects of a freeze-dried water extract of rye.

It is well known that rye is high in dietary fiber, mainly pentosans. Due to the resistance to host enzymes, pentosans in rye increase fecal dry matter excretion, thereby decreasing DM metabolizability. Gohl and Gohl (1977) investigated the influence of a number of hydrocolloids on the transit time of digesta, stool weight and color of stools in rats. All hydrocolloids tested gave the stools a lighter color and increased fecal bulk and water content. Further studies should be carried out to test the nutritional significance of the increased fecal weight caused by the ingestion of dietary fiber. For example, it should be established whether or not the fibers present in digesta decrease the absorption of other nutrients by reducing the physical contact with the absorptive epithelium in the gut.

III. Pattern of Electrolyte Excretion in Roosters Fed Experimental Diets

A. Dietary and urinary electrolyte concentrations and development of diuresis

The results of analyses for electrolyte concentrations in ingredients and diets used in the current experiment are recorded in Table 10. For some reason, the sodium content of the corn used throughout this study was unusually higher than normal values resulting in some unexpected differences in sodium contents among experimental diets. As a result of the water extraction process, sodium, potassium and chloride concentrations in the water-extracted rye were considerably lower than those of non-extracted rye, apparently reflecting the influence of the process in this regard.

Table 10. Ion concentrations of ingredients and diets used in Experiment 2[1]

	% as fed basis		
	Na	K	Cl
Ingredients;			
Corn	0.08	0.43	0.36
Rye	0.01	0.51	0.13
Water-extracted rye	0.005	0.22	0.02
Diets[2];			
1.0% C	0.49	0.79	1.08
1.0% R	0.41	0.88	0.84
1.0% E	0.47	0.96	1.00
1.0% W	0.40	0.61	0.75
0.4% C	0.25	0.73	0.36
0.4% R	0.18	0.85	0.31

[1] Analyzed values.

[2] For full description refer to Materials and Methods (page 50-52).

As mentioned earlier, two roosters out of three birds fed the 1.0% W diet and two out of four birds fed the 0.4% R diet developed varying degrees of diuresis. The diuresis contributed to increased variability in various urinary parameters among roosters within these treatments as can be seen from the relatively large standard errors for these treatment means (Table 11). The osmolality of urine from birds fed the 1.0% W diet was significantly lower than that of 1.0% R treatment indicating the influence of water extraction process in this regard. No significant differences were found, however, in either urine volume or osmolality between 0.4% C and 0.4% R treatments perhaps because of the high variability of the latter group of birds. The osmotic concentrations of urine from diuretic birds were lower (110-290 mosm) than those from normal birds (350-538 mosm), indicating that the cause of diuresis occurred during this study was a lack of antidiuretic hormone (ADH) rather than due to the osmotic diuresis. The secretion of ADH is inhibited when plasma osmolality falls below normal as discussed previously. The major function of ADH in the kidney is to control the permeability of distal tubules and collecting ducts to water in response to the changes in plasma osmolality. When ADH is absent in the circulation of the body, the permeability of these parts of the kidney to water becomes very poor, resulting in the excretion of very dilute urine on the one end and increased plasma osmolality on the other. Although no data are available for ADH activity in diuretic birds encountered in this study, the cause of the diuresis observed appears to be due to the lack of solute ingestion, especially sodium.

The data of urinary sodium concentrations support the above view

Table 11. Urinary volume, osmolality and electrolyte composition of colostomized roosters[1]

Diet treatments[2]	Volume (μl/kg/min)	Osmolality (mosm/ℓ H_2O)	Na^+ (meq/ℓ)	K^+ (meq/ℓ)	Cl^- (meq/ℓ)
1.0% C	60.0±8.66	505 ± 48.2^{a}	112 ± 14.7^{a}	67 ± 13.4^{ab}	157 ± 13.4^{a}
1.0% R	42.1±6.01	541 ± 37.2^{a}	67 ± 16.0^{b}	70 ± 16.0^{ab}	144 ± 8.3^{a}
1.0% E	54.3±6.93	455 ± 21.2^{ab}	73 ± 9.6^{b}	89 ± 20.3^{a}	128 ± 6.1^{a}
1.0% W	170.7±15.65	274 ± 48.8^{b}	32 ± 12.1^{bc}	18 ± 5.1^{b}	69 ± 18.9^{b}
0.4% C	44.3±2.31	518 ± 20.4^{a}	73 ± 3.6^{b}	87 ± 7.2^{a}	114 ± 13.5^{a}
0.4% R	91.9±35.52	338 ± 92.0^{ab}	7 ± 2.9^{c}	45 ± 6.7^{ab}	58 ± 16.5^{b}

[1] $\bar{X}$ ± S.E. (Means within a column with a common or no superscript are not significantly different at 5% level).

[2] For full description refer to Materials and Methods (page 50-52).

regarding the development of diuresis. The most remarkable fact regarding the electrolyte composition of urine was that urinary sodium concentrations from diuretic birds were considerably lower than those from normal birds. In fact, one bird, from the 0.4% R treatment, with severe diuresis reduced the urinary sodium concentration to a level of practically zero. The average volume and osmolality of urine from this bird were 196 $\mu\ell$/min/day and 117 mosm/ℓ H_2O, respectively. In addition, this bird lost body weight very rapidly (1.67 kg to 1.25 kg in a few days) due mainly to dehydration.

Sodium ions present in tubular fluid play an essential role, like ADH, in preventing the development of the diuresis as can be seen in Figure 1. This figure shows transport of sodium and water from the tubule into the spaces surrounding the epithelial cells. Once the sodium enters intercellular spaces by passive absorption mechanism, it is pumped out to the labyrinth of channels at the bases of the epithelial cells by active absorption. Then it can move either forward through the basement membrane into the peritubular capillary or backward into the tubular lumen. One of the major factors that determines the direction of sodium movement at this point is the balance of hydrostatic and colloid osmotic pressures at the capillary membrane. The movement of water closely follows that of sodium even against the concentration gradient of water by the solute-linked water flow mechanism proposed and proved by several workers (Curran and Solomon, 1957; Parsons and Wingate, 1961; Curran and MacIntosh, 1962).

When sodium is deficient in the body, the plasma osmolality decreases because sodium is the major osmolar substance in the plasma fluid.

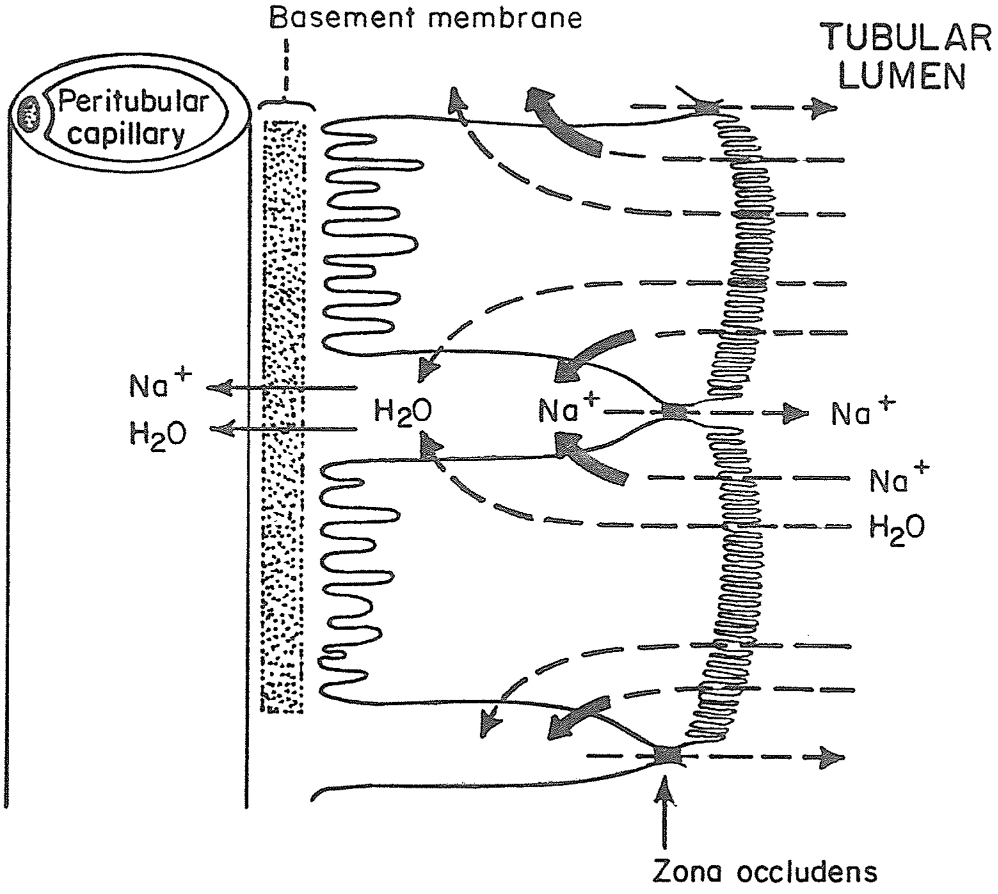

Figure 1. Absorption of fluid at the peritubular capillary membrane.
(From Guyton, A.C. : Textbook of Medical Physiology, 5th Ed., W. B. Saunders Co., 1976).

The secretion of ADH ceases responding to the lowered plasma osmolality. However, the body has the remarkable ability to compensate the deficient sodium through tubular reabsorption of sodium (Orent-Keiles and McCollum, 1940). Water reabsorption is decreased due to the absence of ADH. The reduced level of sodium in the tubular fluid caused by the increased tubular reabsorption of sodium prevents the water reabsorption further because the solute-linked water flow mechanism does not operate any longer. Since the data for ADH activity in diuretic birds encountered in the current experiment were not available, it was impossible to estimate the significance of the role played by ADH in this type of diuresis.

The reduced reabsorption of water at the tubular level in diuretic birds causes two effects: (1) the previously lowered plasma osmolality to return to normal, and (2) dehydration due to the loss of water from the body. Fortunately birds seem to be more resistant to the loss of body water than mammals due to their much greater capacity for fluid mobilization from the skeletal muscle to restore the plasma volume (Djojosugito _et al_., 1968; Wyse and Nickerson, 1971; Harris and Koike, 1977). It is interesting to note in Table 11 that the sodium concentrations in urine from birds fed diets supplemented with the 1.0% dietary salt were significantly higher than those from birds fed diets containing 0.4% dietary salt. This result indicates the ability of the birds to control the urinary excretion of sodium in response to the necessity of the body. A similar observation was made with rats by Orent-Keiles and McCollum (1940).

There were no particular trends in the potassium concentration in urine except that urine from birds fed the 1.0% W diet was low in potassium in comparison to other treatment groups. In terms of urinary chloride concentration, birds fed the 1.0% W diet excreted urine significantly lower in chloride than did birds fed the 1.0% C, 1.0% R and 1.0% E diets. Significant differences in urinary chloride concentration were found between 0.4% C and 0.4% R treatments, and between 1.0% R and 0.4% R treatment groups. Interestingly birds fed the 1.0% W diet excreted urine low in all ions tested. No explanation is available for this phenomenon except that the 1.0% W diet contained relatively low levels of potassium and chloride (Table 10). It appears that the water extraction process removes considerable amounts of various solutes from rye along with the other organic water-soluble substances.

B. Electrolyte concentrations of dried excreta and feces

Data are summarized for electrolyte concentrations of dried excreta and feces in Table 12. The sodium contents of dried excreta from birds fed diets supplemented with the 1.0% salt were significantly higher than those from birds fed diets containing 0.4% salt. In addition, rye-fed birds voided excreta significantly lower in sodium concentration than did corn-fed birds at both levels of salt supplementation. In the case of dried feces, however, there were no significant differences in sodium content among dietary treatments except that the value for the 0.4% R treatment was significantly lower than those of all other treatments. No significant difference was found, however, between 0.4% C and 0.4% R treatments in this regard. The existence of marked dietary influence on excreta ionic content but not on fecal ionic content is an indication that the urine is much more significant than feces with regard to the

Table 12. Electrolyte concentrations of dried excreta and feces from roosters fed experimental diets[1]

Diet treatments[2]	Dried excreta (%)			Dried feces (%)		
	Na	K	Cl	Na	K	Cl
1.0% C	$2.08 \pm .054^{a}$	$3.10 \pm .091^{ab}$	$2.21 \pm .003^{a}$	$0.98 \pm .103^{a}$	$1.85 \pm .207^{ab}$	$0.47 \pm .020$
1.0% R	$1.33 \pm .073^{c}$	$2.91 \pm .091^{bc}$	$1.59 \pm .122^{b}$	$1.02 \pm .136^{a}$	$2.47 \pm .139^{a}$	$0.39 \pm .040$
1.0% E	$1.72 \pm .046^{b}$	$3.43 \pm .200^{a}$	$2.22 \pm .082^{a}$	$1.04 \pm .073^{a}$	$1.58 \pm .128^{b}$	$0.49 \pm .091$
1.0% W	$1.39 \pm .010^{c}$	$2.07 \pm .113^{d}$	$1.53 \pm .050^{b}$	$0.84 \pm .131^{a}$	$1.77 \pm .365^{ab}$	$0.31 \pm .042$
0.4% C	$0.97 \pm .020^{d}$	$2.82 \pm .045^{bc}$	$1.31 \pm .061^{c}$	$0.63 \pm .095^{ab}$	$1.50 \pm .126^{b}$	$0.39 \pm .023$
0.4% R	$0.50 \pm .034^{e}$	$2.57 \pm .144^{c}$	$0.78 \pm .019^{d}$	$0.41 \pm .013^{b}$	$2.35 \pm .164^{a}$	$0.24 \pm .037$

[1] $\overline{X}$ ± S.E. (Means within a column with a common or no superscript are not significantly different at 5% level).

[2] For full description refer to Materials and Methods (page 50-52).

ionic composition of excreta in intact birds. When the dietary salt level increased from 0.4% to 1.0%, the sodium contents of feces and excreta increased significantly in birds fed both corn and rye diets except feces from corn-fed birds. This was also true for urinary sodium concentration as discussed above (Table 11). These data are in agreement with that of Hurwitz et al. (1970) who reported a generally higher sodium concentration in the ileal contents in birds fed a high sodium diet (0.15% Na) in comparison with birds fed a low sodium diet (0.07% Na).

The significant influence of urine on potassium concentration of excreta can also be noted as shown in Table 12. The trend of excreta potassium concentration is quite different from that of feces. The potassium concentration of dried feces in 1.0% R was significantly higher than that found in 1.0% E treatment. However, this trend was reversed in the potassium concentration of dried excreta. Excreta potassium concentration in 1.0% W showed significantly lower level than did any other treatments probably due to the extremely low level of urinary potassium concentration in that treatment. No satisfactory explanation is available yet for these observations except that the 1.0% W diet contained the lowest level of potassium owing to the reduced level of potassium in the water-extracted rye. The fecal potassium content in 0.4% R was significantly higher than that of 0.4% C treatment. This difference disappeared in the case of excreta potassium contents again reflecting the influence of urine.

The pattern of chloride concentration in feces and excreta was very similar to that of sodium. This tendency was also true in urine with minor exceptions as shown in Table 11. These similarities might indicate that the chloride ion follows the movement of sodium ion closely in the body fluids to maintain acid-base balance in the body. Several researchers have expressed similar views which ascribed to sodium and chloride the role of alkalogenic and acidogenic agent, respectively (Nesheim et al., 1964; Cohen et al., 1972; Hurwitz et al., 1973).

C. Balance of electrolyte in intact roosters

Data of electrolyte balance are summarized in Table 13. The data were extremely variable as evidenced by the relatively large standard error values. It was possible, however, to detect some significant differences among treatment comparisons.

The birds fed the 1.0% W diet retained a significantly larger amount of sodium than did birds fed the 1.0% C diet. This trend was opposite to that for urinary sodium concentrations as discussed above, indicating a reciprocal relationship between these two parameters. The high urinary concentration of sodium might mean that the body tries to get rid of those excessive sodium ions via urine. According to Orent-Keiles and McCollum (1940), the rat kidney has the ability to retrieve sodium from urine by the process of tubular reabsorption when sodium is deficient. No published data are available for poultry in this respect.

Roosters fed the 1.0% R diet lost significantly higher potassium than did birds fed the 1.0% W diet. The value for potassium balance in the latter were highly positive indicating that potassium was retained in the body. It should be remembered at this point that the potassium concentration in urine from birds fed 1.0% W diet was lower than others, in-

Table 13. Balance of electrolytes in intact roosters fed experimental diets[1]

Diet treatments[2]	mg/bird/day Na	K	Cl
1.0% C	-43.5 ± 8.54^{b}	-10.6 ± 23.73^{ab}	427 ± 33.0^{a}
1.0% R	-17.8 ± 14.81^{ab}	-57.9 ± 11.76^{b}	276 ± 57.5^{b}
1.0% E	-7.4 ± 21.32^{ab}	16.3 ± 18.69^{ab}	272 ± 15.2^{b}
1.0% W	21.2 ± 0.83^{a}	40.9 ± 20.83^{a}	262 ± 6.4^{b}
0.4% C	0.9 ± 2.52^{ab}	5.0 ± 12.37^{ab}	19.1 ± 8.01^{c}
0.4% R	7.4 ± 12.79^{ab}	-14.8 ± 14.17^{ab}	32.9 ± 8.15^{c}

[1] $\overline{X}$ ± S.E. (Means within a column with a common superscript are not significantly different at 5% level).

[2] For full description refer to Materials and Methods (page 50-52).

dicating again that some relationships might exist between urinary electrolyte concentrations and the balance of these electrolytes in the body.

The mean values for chloride balance of birds fed diets supplemented with 1.0% salt were surprisingly large positively in comparison with any other electrolyte balance data listed in Table 13. One possible explanation for this paradox is that the diets supplemented with 1.0% salt were found (Table 10) to contain excessive chloride (0.75-1.08%) compared to the minimum requirement of chloride by the chicken (0.08%) recommended by NRC (1977). When the dietary salt level was reduced to 0.4% in both corn and rye diets, the dietary chloride concentrations were 0.36% and 0.31%, respectively, and the chloride retention values decreased significantly.

D. Routes of electrolyte excretion in colostomized roosters

Ratios of fecal ion excretion to urinary ion excretion were calculated to see the pattern of ion excretion in colostomized roosters. Unfortunately, only partial data were available as shown in Table 14 because the fecal DM outputs for an 8-hour collection period, during which time urine was also collected, were not measured in 1.0% dietary salt treatments.

As might be expected from the data of dry matter metabolizability of experimental diets listed in Table 8, colostomized roosters fed the 0.4% R diet voided significantly more fecal dry matter than did birds fed the 0.4% C diet for an 8-hour collection period. The ratio of fecal sodium excretion to urinary sodium excretion in birds fed the 0.4% C diet was significantly lower than that in birds on the 0.4% R diet. This result indicates that the major route of sodium excretion in corn-fed birds is

Table 14. Ratio of fecal ion excretion to urinary ion excretion during an 8-hour collection period in colostomized roosters[1]

Diet treatments	Replicates	Output of fecal dry matter g/8 hrs	Feces/urine Na	Feces/urine K	Feces/urine Cl[4]
0.4% C (0.4% salt-corn diet)	1	2.79	0.39	0.81	0.18
	2	4.52	0.34	0.40	0.10
	3	4.01	0.47	0.51	0.11
	4	3.86	0.59	0.46	0.09
	$\bar{X}$ ±S.E.	3.80^{b} ±0.364	0.45^{b} ±.055	0.55^{b} ±.091	0.12 ±.020
0.4% R (0.4% salt-rye diet)	1	7.60	3.25	2.96	0.18
	2	9.32	5.54	3.03	0.21
	3[2]	9.49	6.20	3.61	0.38
	4[3]	5.16	6.41	0.43	0.08
	$\bar{X}$ ±S.E.	7.80^{a} ±1.006	5.35^{a} ±0.724	2.51^{a} ±0.708	0.21 ±.062

[1] a > b ($P \leq 0.05$).

[2] Bird with a mild diuresis.

[3] Bird with a severe diuresis.

[4] No significant difference was found between treatments.

via urine while feces is the major excretory outlet of sodium in rye-fed birds. The sodium concentration of dried feces from birds fed the 0.4% C diet was not significantly different from that from birds fed the 0.4% R diet as was shown in Table 12. However, the sodium concentration in urine from the 0.4% C treatment was significantly higher (10-fold) than that from the 0.4% R treatment while there was no significant difference in urine volumes between these two treatments (Table 11). These facts would explain clearly why there is such a big difference in the excretory pattern of sodium ion between corn-fed birds and rye-fed ones. This result is very similar to that reported by Koike _et al_. (1964) who studied the influence of diet on route of sodium and water excretion in colostomized chickens. When diets low in indigestible residue were fed, sodium excretion was predominantly via urine. However, sodium was excreted mainly via feces when a high residue diet was fed. Based on the data of dry matter metabolizability in Tables 9 and 14, a corn diet could be considered as a diet low in indigestible residue and rye-diet as a high residue diet.

It is of interest to note that no significant difference was found in fecal sodium concentration (Table 12) even though both the outputs of fecal dry matter for 8 hours and the dry matter metabolizabilities are significantly different between 0.4% C and 0.4% R. These results indicate that the sodium present in high fiber diets are less well absorbed in the gut than those in low fiber diets. On the other hand, the sodium present in low residue diets are well absorbed and utilized in the body and the excessive sodium in the body is excreted via urine elevating the sodium concentration of urine from the birds on low residue diets. Therefore, it appears that birds fed high fiber diets are more prone to sodium deficiency than are birds fed low fiber diets, especially when fed a marginally low level of salt. In fact, Slinger et al. (1950) reported that the salt requirement increased progressively from 0.25% to 2.0% as the level of fiber increased, indicating a highly positive relationship between salt requirement and dietary fiber.

Information on the mechanism of inhibition of sodium ion absorption in the gut by dietary fiber is very limited. McConnell et al. (1974) and Eastwood (1977) have suggested a possibility that the lower gut filled with dietary fiber is acting as a chromatography column with adsorptive, monofunctional weak cation exchange resin. If this is true, then the sodium concentration in the feces from birds fed a high fiber diet would be higher than that from birds fed a diet low in dietary fiber. This possibility was ruled out in the current experiment by the fact that no significant difference was found in fecal sodium concentration between rye-fed roosters and corn-fed birds (Table 12).

Another probable mechanism of inhibition of sodium ion absorption is that the dietary fiber present in the digesta may play a role as a physical barrier to the movement of sodium ion in the gut, especially when the digesta is in a gel state. Whether water-soluble or not, dietary fibers increase the digesta weight due to their resistance to host digestive enzymes, thereby decreasing the chance of sodium ions to physically contact with the absorptive epithelium. The deleterious effect of dietary fiber in the absorption of sodium ions and other nutrients would become more prominent if the major absorption site of a nutrient happens to be in the lower gut. Sodium ions (Hurwitz et al., 1970), bile acids (Dietschy, 1968) and amino acids (Hudson et al., 1971) are some examples of these nutrients. More in depth studies are needed to elucidate the mechanisms involved in the inhibition of sodium ion and/or other nutrients by dietary fibers.

As discussed earlier, fecal potassium concentration (Table 12) was significantly lower and urinary potassium concentration was relatively higher in birds fed the 0.4% C diet than those from birds fed the 0.4% R diet. It was not difficult, therefore, to predict the difference between these two dietary treatments. The ratio of fecal potassium excretion to urinary excretion in birds fed the 0.4% C diet was significantly lower than that in birds fed the 0.4% R diet, resembling the pattern of sodium excretion.

It is of interest to note that the bird of a severe diuretic case from the 0.4% R treatment showed remarkably different pattern in potassium excretion from normal birds and/or the mildly diuretic bird fed the same diet. The ratio was very similar to those of the 0.4% C treatment rather than to those of its own group, because the severely diuretic bird decreased fecal potassium concentration while increasing the urinary potassium concentration significantly. Diuresis also appeared to cause a similar effect in the pattern of chloride excretion. No significant difference was found in the chloride excretion pattern between 0.4% C and 0.4% R treatments probably due to the variation caused by the diuretic bird. The effect of diuresis on the pattern of ion excretion remains to be investigated.

IV. Plasma Clearances of Free Water and Electrolyte in Colostomized Roosters

A. Ionic composition of plasma and packed cell volume

As shown in Table 15, no significant differences were found among dietary treatments in osmolality or ionic composition of plasma. This result is in agreement with that reported by Harris and Koike (1977). These researchers found little change in plasma osmolality or electrolyte concentrations between pullets fed a sodium deficient diet (0.017% Na) and a control diet (0.2% Na). On the other hand, Pang _et al_. (1978) observed low plasma sodium, chloride and osmolal concentrations in poults fed a low sodium diet (0.05% Na). Depressed plasma sodium levels have also been observed in Japanese quail fed a diet containing 0.04%-0.05% sodium (Lumijarvi and Vohra, 1976).

Orent-Keiles and McCollum (1940) found that the rat kidney had the capability to retrieve sodium by reducing urinary sodium excretion to a very low level when rats were fed a diet deficient in sodium. The capability of the rat kidney to reduce the urinary excretion of potassium and chloride was also found to be true by Orent-Keiles and McCollum (1941) and Greenberg and Cuthbertson (1942), respectively. According to Buckalew _et al_. (1967), the sodium transport system in the ascending limb of the loop of Henle is unsaturable up to the highest rate of sodium delivery to the loop of Henle that can be achieved in the intact animal. Harris and Koike (1977) found that the administration of furosemide to pullets decreased plasma sodium levels and ECFV significantly while increasing the consumption of water. Furosemide is a diuretic which inhibits carrier systems, especially sodium, in the tubular cells thereby

Table 15. Osmolality and ionic composition of plasma from colostomized roosters fed experimental diets[1,2]

Diet treatments[3]	Osmolality (mosm/ℓ H_2O)	Na^+ (meq/ℓ)	K^+ (meq/ℓ)	Cl^- (meq/ℓ)
1.0% C	311±1.5	158±2.3	4.7±.09	111±.7
1.0% R	310±3.6	151±3.1	4.8±.21	109±1.7
1.0% E	308±3.3	154±1.2	4.8±.24	109±4.5
1.0% W	307±2.6	157±1.6	4.7±.25	113±4.5
0.4% C	309±1.9	149±1.1	5.2±.52	107±2.0
0.4% R	309±1.8	149±2.2	4.5±.25	108±1.5

[1] $\bar{X}$ ± S.E.

[2] No significant difference was found in any parameters among dietary treatments.

[3] For full description refer to Materials and Methods (page 50-52).

increasing osmotic pressure and causing osmotic diuresis. The buffering capacity of the kidney which seems to maintain body homeostasis in the midst of varying environmental conditions appears to be largely responsible for the consistent blood parameters shown in Table 15.

The packed cell volume (PCV) data obtained with roosters before and after colostomy are shown in Table 16. Also shown are the results of a series of t-tests and a paired t-test. Whether intact or colostomized, the birds did not respond significantly either to the various types of dietary grains or to the different dietary salt levels. It appears that either the 0.4% dietary salt was not low enough or 1.0% salt addition was not high enough to induce changes in PCV. Elevated PCV values were reported in growing Japanese quail (Lumijarvi and Vohra, 1976) and in young poults (Pang _et_ _al_., 1978) when fed sodium-deficient diets. However, 13-week old pullets fed a sodium-deficient diet did not show any change in PCV values (Harris and Koike, 1977). This disagreement might be due to the fact that young birds are more sensitive than old birds to changes in salt intake as reviewed and proved by Pang (1975).

It is of interest to note that a significant difference was detected in PCV between intact and colostomized birds when a paired t-test was conducted utilizing the mean values of each treatment as replicates. The cause of the decrease in PCV due to colostomy operation is not readily apparent but it may be related to the increased water intake (Table 6) and/or to the decreased plasma osmotic concentration (Table 8) of the colostomized birds.

Table 16. Packed cell volume in roosters before and after the colostomy operation[1,2]

Diet treatments[3]	Intact birds (%)	Colostomized birds (%)	t-test
1.0% C	34.9±1.59	29.3±1.36	N.S.
1.0% R	36.3±1.66	29.4±1.29	$P \leq 0.05$
1.0% E	37.2±2.08	32.9±0.98	N.S.
1.0% W	34.6±1.87	31.0±0.81	N.S.
0.4% C	30.4±2.47	29.8±0.80	N.S.
0.4% R	32.3±0.63	28.9±1.74	N.S.
$\overline{X}$ ± S.E.	34.3±1.03	30.2±0.61	$P \leq 0.05$[4]

[1] $\overline{X}$ ± S.E.

[2] No significant differences were found among dietary treatments either in intact roosters or in colostomized birds.

[3] For full description refer to Materials and Methods (page 50-52).

[4] Paired t-test.

B. Plasma clearances of osmols, free water and electrolytes

The plasma clearance of any substance is defined as the volume of plasma required to supply the amount of that substance appearing in the urine during any unit time period. It is used to express the ability of the kidneys to clear the plasma of various substances. The concept of plasma clearance is important because it is an excellent measure of kidney function. Unfortunately data regarding plasma clearances in birds are extremely limited.

The mean values for plasma clearances of osmols, free water and electrolytes in colostomized birds are shown in Table 17. For the purpose of comparison, similar plasma clearance values were calculated from the data reported by Skadhauge and Schmidt-Nielsen (1967a) and are summarized in Table 18. It should be kept in mind that these values were obtained with birds with exteriorized colon and/or ureters so that urine would not make retrograde movement into the large intestine where most of the post-renal modification of urine is known to occur. Therefore, plasma clearance values obtained with intact birds, if technically feasible, might be different from those listed in Tables 17 and 18. It was assumed in this experiment, however, that any trend in plasma clearance values obtained with colostomized birds would also be evident in intact birds.

The C_{osm} of the 1.0% C treatment was significantly higher than those from any other treatment except the 1.0% E treatment. It is of interest to note that the C_{osm} from birds fed corn diets increased significantly when the salt level increased from 0.4% to 1.0% while the C_{osm} from rye-fed birds remained the same for both salt levels. The water extraction

Table 17. Plasma clearance of osmols, free water and electrolytes in colostomized roosters fed experimental diets[1]

Diet treatments[2]	Plasma clearance (μℓ/kg/min)				
	C_{osm}	C_{H_2O}	C_{Na^+}	C_{K^+}	C_{Cl^-}
1.0% C	94 ± 6.6^a	-35±5.4	42 ± 4.8^a	824±108.4	83 ± 5.0^a
1.0% R	71 ± 6.9^b	-28±4.5	18 ± 2.8^b	563±60.7	54 ± 5.9^{ab}
1.0% E	77 ± 6.5^{ab}	-23±1.8	25 ± 4.6^b	937±126.0	64 ± 12.1^{ab}
1.0% W	57 ± 1.7^b	13±15.4	12 ± 3.2^{bc}	237±19.5	37 ± 5.4^b
0.4% C	68 ± 6.8^b	-27±3.4	20 ± 3.0^b	720±146.3	45 ± 2.7^b
0.4% R	71 ± 1.9^b	21±34.6	3 ± 0.5^c	1133±667.9	35 ± 3.5^b

[1] $\bar{X}$ ± S.E. (Means within a column with a common or no superscript are not significantly different at 5% level).

[2] For full description refer to Materials and Methods (page 50-52).

Table 18. Plasma clearances of osmols, free water and electrolytes in roosters[1,2]

Treatments	Plasma clearance (μℓ/kg/min)				
	C_{osm}	C_{H_2O}	C_{Na^+}	C_{K^+}	C_{Cl^-}
Dehydration	28.35	-10.41	14.71	153.0	9.69
Water-loading	110.4	188.0	74.60	364.1	68.63
Salt-loading	192.3	-10.88	176.0	981.4	179.6

[1] Values used in this table were obtained by direct calculation from the data reported by Skadhauge and Schmidt-Nielsen (1967a).

[2] The ureteral urine was collected through polyethylene funnels.

of rye did not affect the C_{osm} value significantly. From a physiological standpoint, high C_{osm} values mean that the birds are loaded with osmotically active particles, and vice versa. As can be seen in Table 18, salt-loaded roosters showed the highest value in C_{osm} while dehydrated birds showed the lowest value.

There were no significant differences in free water clearance (C_{H_2O}) among dietary treatments probably due to the large within treatment variation caused by the diuretic birds in 1.0% W and 0.4% R treatment groups. The C_{H_2O} is important because it determines how rapidly the kidneys change the balance between water and osmotic substances in the body fluids. The C_{H_2O} can be either positive, in which case excess water is being removed; or it can be negative, in which case excess solutes are being removed. Interestingly, diuretic birds in this experiment always showed positive values for C_{H_2O}, the more severe the diuresis the larger the value, indicating that excess water was being removed in these diuretic birds. In birds forcefully loaded with water, the C_{H_2O} value increased tremendously to remove excess water as shown in Table 18. Evaluation of the data collected in the current experiment, however, leads to the conclusion that the diuresis developed in birds from the 1.0% W and 0.4% R treatment groups was caused by salt deficiency.

The plasma clearance of sodium (C_{Na^+}) values listed in Tables 17 and 18 support the conclusion regarding the cause of diuresis. When the dietary salt level decreased from 1.0% to 0.4%, the C_{Na^+} values decreased significantly in both corn-fed birds and rye-fed birds. When roosters were salt-loaded (Table 18), the C_{Na^+} values increased drastically, indicating that excess sodium ion was being removed. When dehydrated, roosters showed greatly reduced C_{Na^+} values, indicating that the birds were salvaging sodium.

The corn-fed birds showed significantly higher C_{Na^+} values than did rye-fed birds regardless of dietary salt levels. The water extraction process of rye did not cause any change in C_{Na^+} but the rye extract decreased C_{Na^+} values significantly when added to a corn diet at a level of 12%. These results indicate that rye contains substances that decrease C_{Na^+} values. In other words, rye-fed birds tend to need more sodium than do corn-fed birds. Although the water-extractable substances present in rye can cause the same effect on C_{Na^+} as rye when freeze-dried and incorporated into a corn diet, most of the substances that decrease C_{Na^+} appear to remain intact in rye, indicating that they are water-insoluble. Fractionation studies of Antoniou (1980) indicated that rye contains approximately 2.1% soluble and 7.9% water-insoluble pentosans. In addition, the same worker claimed that complete removal of antinutritionally active pentosans from rye was impossible as they constituted cell wall components.

The water-extraction process would appear to have two effects on rye: (1) partial elimination of substances that decrease the C_{Na^+}, and (2) removal of much of the water-soluble, osmotically-active particles. The latter effect might explain the lower, although not significant, C_{Na^+} value in the 1.0% W treatment compared to that in the 1.0% R treatment. Furthermore it would also explain why some of the birds fed the 1.0% W diet developed diuresis while the birds on the 1.0% R diet did not. The water-soluble, osmotically-active particles include water-soluble proteins and free electrolytes. Antoniou (1980) found that a freeze-dried rye extract contained 13.4% protein. The rye extract sample used in this experiment was found to contain 4.2% N (26.3% crude protein). The difference in protein content of the freeze-dried rye extracts might be due to differences in the length of extraction time and extraction methodology. As for free electrolytes. data recorded in Table 10 clearly show that the water extraction process decreased electrolyte concentrations in rye.

There were no significant differences in plasma clearance of potassium (C_K+) among treatments. The mean values of C_K+ were remarkably large as compared with the plasma clearance values for the other electrolytes. The high potassium concentration in urine (Table 11) compared with that of plasma (Table 15) explains this phenomenon. A similar trend in C_K+ values was also found in the data presented in Table 18. Potassium, in the presence of aldosterone, is known to be secreted actively in the distal and collecting tubules in exchange for sodium (Guyton, 1976). This active secretory transport of potassium into the distal tubules and collecting ducts in exchange for sodium is important for an animal to keep the plasma potassium concentration at a low level and the plasma sodium concentration at a high level. Buckalew _et_ _al_. (1967) found an intrinsic defect in sodium transport in the ascending limb of the loop of Henle in potassium depleted rats.

The pattern of the plasma clearance of chloride ($C_{Cl}-$) was similar to those of C_{osm} and $C_{Na}+$. When the dietary salt level decreased from 1.0% to 0.4%, the $C_{Cl}-$ values decreased significantly in corn-fed birds. A similar trend was found by Skadhauge and Schmidt-Nielsen (1967a) as shown in Table 18. No significant difference in C_{Cl^-}, however, was found among rye-fed birds in this respect. The water-extraction process and/or the addition of rye extract to a corn diet did not have any influence on the plasma clearance of chloride.

In conclusion, rye contains substances that inhibit electrolyte absorption, especially sodium, from the gut. These substances can be partially eliminated by the process of water extraction, but most of them remain intact in rye. When birds are fed diets containing these substances, they need more salt, especially sodium, in the diet to maintain normal economy of salt and water. The avian kidneys appear to function similarly to the mammalian kidney to maintain homeostasis in the body by controlling tubular reabsorption and secretion of electrolytes and water. Diuresis and/or antidiuresis are the results of the essential functions of the kidney.

V. Some Physical Properties of Experimental Diets and Excreta and Fecal Samples

A. Viscosity of diets, excreta and fecal fluids

The mean viscosity values for diet extracts and excreta and fecal fluids are shown in Table 19. Diet extracts were prepared by centrifuging a mixture of 1 g of the finely ground diet and 9 mℓ of distilled water at 12,000 rpm for 10 min. The mixture was kept overnight at 4°C before being centrifuged. Rye diets displayed remarkably high viscosity as compared with corn, corn plus rye extract or water-extracted rye diets. The data indicate that rye contains substances that possess viscous characteristics in water. In addition, the water extraction process of rye markedly reduced the content of these substances in rye,

Table 19. Viscosity of diet extracts, and excreta and fecal fluid from roosters fed experimental diets[1]

Diet treatments[2]	Diet extracts[3] (cP)	Fresh excreta fluid (cP)	Fresh fecal fluid (cP)
1.0% C	0.94	1.19±.084^c	5.77±.064^b
1.0% R	2.94	2.78±.528^b	21.65±5.314^a
1.0% E	1.30	1.43±.085^c	5.21±.725^b
1.0% W	1.14	1.35±.089^c	8.46±2.175^b
0.4% C	1.02	1.60±.216^c	5.82±.952^b
0.4% R	2.99	8.62±.382^a	27.72±2.846^a

[1] $\overline{X}$ ± S.E. (Means within a column with a common superscript are not significantly different at 5% level).

[2] For full description refer to Materials and Methods (page 50-52).

[3] Diet extracts were prepared by centrifuging a mixture of 1 g of finely ground diet and 9 ml of distilled water at 12,000 rpm for 10 min. The mixture was kept overnight at 4°C prior to centrifugation.

indicating that the substances are water-soluble. However, a rye extract (freeze-dried) did not increase viscosity greatly when added to a corn diet at a level of 12%.

The viscosities of excreta fluids from birds fed rye diets were significantly higher than those from birds fed corn, corn + rye extract, or water-extracted rye diets. Fernandez _et_ _al_. (1973b) and Misir and Marquardt (1978b) reported similar findings in that rye-fed chickens excreted excreta of a more viscous nature than did controls, and this sticky excreta condition disappeared when rye was extracted with water. Antoniou (1980) indicated the water-soluble substances present in rye that cause the sticky excreta condition consist primarily of pentosans. These pentosans which have hydrocolloidal properties are resistant to host digestive enzymes and, therefore, are grouped as dietary fiber (Trowell _et_ _al_., 1976). The freeze-dried rye extract did not increase the viscosities of excreta or fecal fluids significantly when added to a corn diet at a level of 12%. This is contradictory to the findings of Fernandez _et_ _al_. (1973b) and Misir and Marquardt (1978b) who observed the sticky excreta condition in young chickens fed control diets containing a dried rye extract. A possible explanation for this discrepancy is that the researchers cited above used young chickens as experimental animals while adult roosters were used in the current experiment. No significant difference was found in excreta fluid viscosity between 1.0% C and 0.4% C treatments. However, for some reason, the viscosity of excreta fluid from birds fed the 0.4% R diet was significantly higher than that from birds fed 1.0% R diet. No explanation is available for this observation.

The viscosities of fecal fluids were considerably higher than those of excreta fluids. It is obvious that the urinary water decreased the viscosity of the excreta fluid. Again, the rye-fed roosters excreted significantly more viscous feces than did birds fed corn, corn plus rye extract and water-extracted rye diets. In contrast to the data for excreta fluids, no significant difference was found in the viscosity of fecal fluids between 1.0% R and 0.4% R treatments.

B. Water holding capacity and bulk density of grain samples and dried feces

One of the physical properties of dietary fiber is that it can hold and/or adsorb considerable amounts of water. The water holding capacity (W.H.C.) of dietary fiber depends on the chemical composition, spatial configuration, degree of branching and on the orientation and availability of polar groups (carboxyl, hydroxyl, etc.). Polar groups present in dietary fiber have the ability to bind water and form a semi-rigid, jelly-like structure with concomitant swelling and increase in viscosity. These hydrocolloidal properties of dietary fiber would be expected to decrease the absorption of nutrients by the gut because of dilution and decreased rate of diffusion of nutrients toward the intestinal mucosa (Kay and Strasberg, 1978). In addition, McConnell _et al_. (1974) indicated a possible influence of the W.H.C. of dietary fiber on bowel function.

A limited number of techniques have been established to measure the W.H.C. of water-insoluble dietary fiber (McConnell _et al_., 1974; Takeda and Kiriyama, 1979). These techniques, however, are not suitable for samples high in water-soluble dietary fiber such as rye or barley. A modified technique, which was relatively simple, was used in the current experiment. Data obtained are summarized in Table 20. The W.H.C. of rye was determined to be 1.22 mℓ/g DM whereas corn and water-extracted rye showed lower values (0.90 and 0.94 mℓ/g DM, respectively). Fecal samples from corn-fed roosters displayed significantly less W.H.C. than did those from rye-fed birds. The dietary salt level did not affect the W.H.C. of dried fecal samples. Feces from birds fed the water-extracted rye diet had a W.H.C. as high as that obtained for rye-fed birds whereas the addition of the rye extract to the corn diet did not have an influence regarding W.H.C. The original intention for measuring the W.H.C. of feces was to determine whether a relationship existed between fecal moisture content (Table 5) and W.H.C. of dried fecal samples. No clear-cut relationship, however, was apparent as a result of the comparison between these two parameters.

During the conduct of Experiment 2, it was repeatedly observed that fresh feces from birds fed diets based on rye or water-extracted rye were bulkier than those from corn-fed birds. Furthermore, the dried feces from the former looked fluffier than those from the latter. These characteristics of feces from birds fed diets based on rye or water-extracted rye appeared to be due to the dietary fiber present in the diets. Bulk density of dietary grains and dried fecal samples was measured in an attempt to quantify dietary treatment effects. The differences in bulk density among grain samples were relatively small as can be seen in Table 20. Significant differences, however, were found among dried fecal samples. Fecal samples from birds fed corn diets (including the 1.0% E diet) showed significantly higher bulk densities

Table 20. Water holding capacity and bulk density of grain samples and dried feces from roosters[1]

Samples	Water holding capacity (mℓ/g D.M.)	Bulk density (D.M. g/mℓ)
Grains;		
Corn	0.90	0.66
Rye	1.22	0.65
Water-extracted rye	0.94	0.67
Feces[2];		
1.0% C	$2.79 \pm .093^{b}$	$0.71 \pm .015^{a}$
1.0% R	$3.22 \pm .065^{a}$	$0.55 \pm .003^{b}$
1.0% E	$2.62 \pm .076^{b}$	$0.67 \pm .018^{a}$
1.0% W	$3.29 \pm .076^{a}$	$0.50 \pm .017^{c}$
0.4% C	$2.70 \pm .048^{b}$	$0.66 \pm .013^{a}$
0.4% R	$3.19 \pm .095^{a}$	$0.56 \pm .012^{b}$

[1] $\overline{X}$ ± S.E. (Means within a column with a common superscript are not significantly different at 5% level).

[2] For full description refer to Materials and Methods (page 50-52).

than did those from rye-fed birds. The bulk density of dried feces from birds fed the water-extracted rye diet was significantly lower than those from rye-fed roosters. A reciprocal relationship was found between W.H.C. and bulk density, the larger the bulk density the smaller the water holding capacity. It is suggested, therefore, that the water holding capacity of a sample is primarily determined by the space occupied by the unit weight of that sample.

Fecal bulk density indirectly estimates the bulk density of digesta in the gut. It is logical to assume that the volume occupied by digesta in the gut is determined by two variables: (1) the DM digestibility of the diet, and (2) the bulk density of the digesta. Digesta from a diet low in DM digestibility will occupy a larger space in the gut than will that from a diet high in DM digestibility. This effect would become increasingly more significant as the digesta reaches the lower gut since at this point most of the digestible nutrients would have disappeared. In terms of bulk density, a digesta would occupy a relatively large space in the gut if the bulk density of the digesta is low. Therefore the effect of dietary fiber on the digesta volume is two-fold. It increases the weight and/or bulk of digesta by simply not being absorbed and increases the digesta volume by decreasing bulk density. If epithelial surface area is assumed to be constant, the nutrients and/or toxic agents contained in a digesta which occupies a large space in the gut would have less chance to be absorbed than would those contained in a digesta which occupies a small space.

VI. Overall Discussion

The diuretic symptoms observed in the colostomized roosters fed the 1.0% W and 0.4% R diets in the current experiment appeared to be due to a deficiency of salt, especially sodium. In addition, the lack of response of intact roosters fed the 1.0% R diet in terms of water intake and excreta moisture content (Table 4) indicated that rye-fed birds are more resistant to excessive salt intake than were corn-fed birds. When colostomized, birds fed the 1.0% R diet excreted urine significantly lower in sodium concentration than did colostomized birds fed the 1.0% C diet. In addition, the former showed a significantly lower plasma clearance of sodium than did the latter. These results lead to the conclusion that rye-fed birds are more prone to sodium deficiency than are birds fed diets based on corn.

Fecal sodium and potassium excretions of rye-fed birds were significantly higher than those of corn-fed birds (Table 14). Although not significant, the fecal chloride excretion appeared to increase when corn was replaced with rye in the diet. This characteristic of rye is attributed to the high dietary fiber content in rye, which inhibits electrolyte, especially sodium, absorption in the gut. The increased fecal weight caused by the dietary fiber present in rye appeared to be responsible for this phenomenon.

The positive relationship between dietary fiber content and fecal weight was reported by several workers (Cummings et al., 1979; Gohl and Gohl, 1977). In a review paper, Eastwood (1977) concluded that the most consistent characteristic of vegetable dietary fiber is its ability to alter stool weight. Ismail-Beigi et al. (1977) found a significant correlation between fecal fiber and the contents of Zn, Ca and Mg in feces. Stephen and Cummings (1979) reported increased fecal nitrogen excretion in man when the dietary fiber intake was increased. A linear relationship was found in pigs between metabolic fecal nitrogen excretion and fecal dry matter output of pigs fed N-free diets (Whiting and Bezeau, 1957). Eastwood (1977) indicated that a large fecal output may have relevance in cholesterol metabolism in that there is a linear relationship between the stool weight, both wet and dry, and the excretion of fecal bile acids. In terms of toxic agents, Ershoff and Marshall (1975) found protective effects of dietary fiber in rats fed toxic doses of sodium cyclamate and polyoxyethylene sorbitan monostearate (Tween 60). Takeda and Kiriyama (1979) investigated the mechanism(s) by which dietary fiber exerts beneficial effects on the growth of weanling rats fed toxic doses of amaranth. These workers found that growth was improved progressively with increasing levels of dietary fiber. It was concluded that the protective activity of various dietary fibers depended on physical properties such as settling volume in water (SV) or water holding capacity. Basically, the SV is the reverse of bulk density measured in the current experiment. All of the experimental evidence presented so far leads to the conclusion that dietary fiber, per se, could materially increase fecal excretion of any dietary constituents by increasing the size and/or weight of feces. In other words, the dietary fiber functions as a diluting agent in the gut, decreasing the absorbabilities of nutrients and/or toxic agents.

The effects of dietary fiber on the fecal excretion of a substance would become more significant if the major absorption site of a nutrient were in the lower gut, i.e., the ileum and the large intestine. The reasoning for this is that in the lower gut most of the digestible nutrients have already disappeared so that the digesta volume is largely determined by the dietary fiber content in the digesta. Furthermore, in the lower gut the digesta resumes a gel state from the previous sol state as the water absorption proceeds making the diffusion of nutrients more difficult.

Several workers have emphasized the role of dietary fiber as a monofunctional weak cation exchange resin (Eastwood and Mitchell, 1976; McConnell _et_ _al_., 1974). If the dietary fiber present in rye functions as a cation exchanger, and therefore increases the fecal sodium excretion, the fecal sodium concentration from rye-fed birds would be higher than those from corn-fed birds. Interestingly, no significant difference was found in fecal sodium concentration between corn-fed roosters and rye-fed birds (Table 11). Consequently, the significance of the role played by rye fiber as a cation exchanger relative to sodium absorption was considered minimal.

The diuretic symptoms noted in colostomized birds fed the 1.0% W diet deserves additional consideration. Clearly, the diuresis was caused by deficient ingestion and/or utilization of solutes even though 1.0% salt was added to the diet. The DM metabolizability of this diet, however, was equivalent to those of corn diets. This paradox could be explained by the fact that the birds fed the 1.0% W diet excreted feces high in fiber even though the dietary fiber content of the 1.0% W diet was low. This could have happened if the water extraction process of of rye improved the digestibility of the water-insoluble, non-fibrous portion of the grain, i.e., starch as was indicated by Naber and Touchburn (1969a, 1969b). The data on bulk density and water holding capacity (Table 20) of feces from birds fed the 1.0% W diet support this view further. The bulk density of feces from the 1.0% W treatment groups was significantly lower than those from birds fed rye diets. Due to its extremely low bulk density, the feces from birds fed the 1.0% W diet would have occupied a considerably large space in the gut, probably hindering the absorption of sodium by reducing the chance of physical contact between intestinal mucosa and sodium ions present in the digesta.

Experimental evidence indicated that the addition of the rye extract to a corn diet at a level of 12% increased the sodium requirement of the birds. Data on the DM metabolizability and fecal bulk density, however, indicate that the tendency toward an increase in sodium requirement of birds fed diets supplemented with the rye extract is not associated with dietary fiber. It is not clear by what mechanism(s) the rye extract increases the sodium requirement of birds fed diets containing a relatively low level of this extract.

SUMMARY

Experiment 2 was conducted to study water and electrolyte metabolism of adult roosters fed either corn or rye diets supplemented with high (1.0%) and low (0.4%) levels of salt. A water-extracted rye diet containing 1.0% dietary salt was used to determine the effect of the water extraction process of rye on water and electrolyte metabolism in the chicken. An attempt was made to determine the effect of a freeze-dried water extract of rye (rye extract) on water and electrolyte metabolism by incorporating the rye extract into a 1.0% salt-corn diet at a level of 12%. Colostomy operation was performed on each bird to facilitate the separate collection of urine and feces.

Water metabolism studies with intact roosters indicated that birds fed rye diets were more resistant to an excessive intake of salt than were birds fed corn diets. Furthermore, studies with colostomized roosters indicated that birds fed rye diets were more sensitive to sodium deficiency than were birds fed corn diets. The major route of sodium excretion in rye-fed birds was via feces while urine was the major excretory pathway of sodium in corn-fed birds. The urinary sodium concentration and the plasma clearance of sodium were lower in rye-fed birds than were those in corn-fed birds, indicating that the rye-fed birds were retrieving sodium through tubular reabsorption.

Intact roosters fed a water-extracted rye diet supplemented with 1.0% salt appeared to drink less and excrete less water than did birds on a rye diet. When the same diet was fed to colostomized roosters, the birds displayed similar sodium deficiency symptoms to those observed

with rye-fed birds. It was concluded, therefore, that the water extraction process did not completely eliminate the substance(s) from rye that causes reduced absorption of sodium in the gut. The addition of a rye extract to a corn diet also tended to reduce sodium absorption.

Dry matter metabolizabilities of rye diets were significantly lower than were those of corn diets indicating that rye is high in dietary fiber. The bulk density (g/mℓ) of feces from rye-fed birds were significantly lower than those from corn-fed birds indicating that the feces from rye-fed birds contained considerable amounts of fiber. Furthermore the bulk density of feces from birds fed the water-extracted rye diet was lower than those from birds fed rye diets. The possible role of dietary fiber and/or fecal fiber in increasing fecal sodium excretion was discussed.

The substance(s) which causes sticky excreta condition among rye-fed birds was found to be water-soluble. When added at a level of 12% to a corn diet, however, a freeze-dried water extract of rye did not increase the viscosity of excreta and/or feces among adult roosters.

The colostomized roosters tended to drink more water than did intact birds. In addition, the colostomized birds required more salt. It was concluded, therefore, that the colon, not the cloaca, plays an important role in the post-renal modification of urine for normal economy of water and salt in intact birds.

Experiment 3

The Effects of the Addition of Graded Levels of Salt on the Performance of Growing Chickens Fed Rye Diets

INTRODUCTION

Slinger *et al*. (1950) reported that the salt requirement of chickens was influenced by several factors, including the level of fiber in the diet. The salt requirement of the growing chicken increased progressively up to 2.0% as low fiber-high energy grains were replaced by high fiber-low energy grains, wheat by-products or cellulose.

Rye can be classified as a high fiber-low energy grain. In addition, evidence from Experiments 1 and 2 indicated that rye-fed birds were more susceptible to salt deficiency than were corn-fed birds.

A series of growth trials were conducted in Experiment 3 to determine if salt, per se, was a contributing factor in the growth-depressing properties of rye in poultry. Two of the three trials were conducted in battery brooders and the third trial in conventional floor pens.

MATERIALS AND METHODS

I. Trial 1

Experimental birds and management. Two hundred one-day-old SCWL cockerels were housed in electrically heated, thermostatically controlled battery brooders with raised wire floors. A continuous lighting scheme was used throughout this experiment. Chickens were reared on a commercial chick-starter diet for 5 days. Thereafter the birds were placed in weight groups from which they were randomly assigned to the experimental groups. Feed and water were supplied *ad libitum*.

Experimental diets and design. A completely randomized design involving 4 dietary treatments, 5 replicates per treatment, 10 birds per replicate, was employed in a 2-week feeding trial. Graded levels of salt (0.3, 0.6 and 0.9%) were added to rye-based diets and a corn diet with 0.3% dietary salt was included as a control. All diets were formulated to be iso-caloric and iso-nitrogenous with a calorie:protein ratio (c/p) of 150. The composition of diets used in Trial 1 is shown in Table 21. Means were assessed statistically by analysis of variance and Student-Newman-Keul's multiple range test as described by Snedecor and Cochran (1967). The limit of probability accepted as being significant was $P \leq 0.05$.

II. Trial 2

Experimental birds and management. One hundred eighty one-day-old White Cornish broiler chickens were housed as in Trial 1. The birds were fed on commercial chick-starter diets for 3 days prior to being fed experimental diets. At the start of the trial the birds were categorized into similar weight groups from which they were randomly assigned to the experimental groups. Feed and water were supplied *ad libitum*.

Experimental diets and design. A completely randomized design with 5 dietary treatments, 4 replicates per treatment, 9 birds per replicate, was used in a 10-day feeding trial. Graded levels of salt (0.3, 0.4, 0.5 and 0.6%) were added to rye-based diets and a corn diet with 0.3% dietary salt was used as a control regime. All diets were formulated

Table 21. Composition of diets used in Experiment 3 - Trial 1

	Diets[1]			
Ingredients	0.3% salt rye	0.6% salt rye	0.9% salt rye	0.3% salt corn
	%			
Corn	-	-	-	68.5
Rye (puma)	73.9	73.9	73.9	-
Soybean oil	4.0	4.0	4.0	-
Soybean meal (47.5%)	9.0	9.0	9.0	15.0
Casein (vitamin-free)	8.0	8.0	8.0	8.0
Celufil[2]	0.6	0.3	-	4.0
Salt (iodinated)	0.3	0.6	0.9	0.3
Biophos[2]	1.6	1.6	1.6	1.6
Limestone	1.6	1.6	1.6	1.6
Vitamin-mineral premix[4]	1.0	1.0	1.0	1.0
	100.0	100.0	100.0	100.0
Sodium content (%)[5]	0.13	0.26	0.34	0.21

[1] All diets were formulated to be iso-caloric and iso-nitrogenous with a c/p ratio of 150.

[2] Non-nutritive bulk supplied by United States Biochemical Corp., Cleveland, Ohio.

[3] Ca 18%, P 21%.

[4] Vitamin-mineral premix provided the following per kg of diet (mg or as designated): MnO_2, 44; ZnO_2, 60; $CuSO_4.5H_2O$, 16; $FeSO_4.7H_2O$, 400; choline-Cl (50%), 1,500; ethoxyquin, 125; thiamine, 2.0; riboflavin, 4.0; Ca-pantothenate, 10.0; niacin, 25; pyridoxine, 3.0; folacin, 0.55; biotin, 0.15; vitamin B_{12}, 0.01; vitamin K, 0.55; vitamin A, 1,500 IU; vitamin D, 800 ICU; and vitamin E, 10 IU.

[5] Analyzed values.

to be iso-caloric and iso-nitrogenous with a c/p ratio of 150. The composition of experimental diets is shown in Table 22. Statistical analysis were done as in trial 1.

III. Trial 3

Experimental birds and management. Eight hundred one-day-old female broiler chickens (Cobb strain) were allotted at random to 16 straw-littered floor pens (1.5 x 4.3 m). All chickens were fed a commercial broiler starter diet for 19 days at which time four dietary regimes were randomly assigned. Feed and water were supplied *ad libitum*.

Experimental diets and design. Four dietary treatments, 4 pens (replicates) per treatment, 50 birds per pen, were employed in this trial. Four broiler starter diets, based on rye, differing only in salt content (0.30, 0.45, 0.60 and 0.75%) were prepared to be iso-caloric and iso-nitrogenous with a c/p ratio of 136 (Table 23). The birds were fed starter diets for two weeks and switched to counterpart finisher diets (Table 24) for a further two-week period at which time the trial was terminated. Broiler finisher diets were similar to broiler starter diets except that the c/p ratio was increased to 151. Statistical analysis was done as in the previous trial.

RESULTS

I. Trial 1

Performance data for young cockerels fed the various experimental diets are shown in Table 25. When the dietary salt level of the rye

Table 22. Composition of diets used in Experiment 3 - Trial 2

Ingredients	0.3% salt rye	0.4% salt rye	0.5% salt rye	0.6% salt rye	0.3% salt corn
	%				
Corn	-	-	-	-	68.5
Rye (puma)	73.9	73.9	73.9	73.9	-
Soybean oil	4.0	4.0	4.0	4.0	-
Soybean meal (47.5%)	9.0	9.0	9.0	9.0	15.0
Casein (vitamin-free)	8.0	8.0	8.0	8.0	8.0
Celufil[2]	0.6	0.5	0.4	0.3	0.4
Salt (iodinated)	0.3	0.4	0.5	0.6	0.3
Biophos[2]	1.6	1.6	1.6	1.6	1.6
Limestone	1.6	1.6	1.6	1.6	1.6
Vitamin-mineral premix[2]	1.0	1.0	1.0	1.0	1.0
Sodium content (%)[3]	0.13	0.18	0.21	0.26	0.21

[1] All diets were formulated to be iso-caloric and iso-nitrogenous with a c/p ratio of 150.

[2] See Table 21.

[3] Analyzed values.

Table 23. Composition of broiler starter diets used in Experiment 3 - Trial 3

	Diets[1]			
Ingredients	0.30% salt	0.45% salt	0.60% salt	0.75% salt
		%		
Rye (puma)	64.50	64.35	64.20	64.05
Fish meal (70%)	6.0	6.0	6.0	6.0
Soybean meal (47.5%)	20.0	20.0	20.0	20.0
Tallow	2.5	2.5	2.5	2.5
Sunflower oil	2.5	2.5	2.5	2.5
Salt (iodinated)	0.30	0.45	0.60	0.75
Biophos[2]	1.6	1.6	1.6	1.6
Limestone	1.6	1.6	1.6	1.6
Vitamin-mineral premix[3]	1.0	1.0	1.0	1.0
	100.0	100.0	100.0	100.0
Sodium content (%)[4]	0.16	0.22	0.28	0.34

[1] All diets were formulated to be iso-caloric and iso-nitrogenous with a c/p ratio of 136.

[2] Ca 18%, P 21%.

[3] Vitamin-mineral premix provided the following per kg of diet (mg or as designated): MnO_2, 44; ZnO_2, 60; $CuSO_4.5H_2O$, 16; $FeSO_4.7H_2O$, 400; choline-Cl (50%), 1,500; ethoxyquin, 125; thiamine, 2.0; riboflavin, 4.0; Ca-pantothenate, 10.0; niacin, 25; pyridoxine, 3.0; folacin, 0.55; biotin, 0.15; vitamin B_{12}, 0.01; menadion, 0.55; vitamin A, 4,000 IU; vitamin D, 1,500 ICU; and vitamin E, 5 IU.

[4] Calculated values based on the analyzed sodium contents of each ingredient.

Table 24. Composition of broiler finisher diets used in Experiment 3 - Trial 3

Ingredients	0.30% salt	0.45% salt	0.60% salt	0.75% salt
	Diets[1]			
	%			
Rye (puma)	70.00	69.85	69.70	69.55
Fish meal (70%)	6.0	6.0	6.0	6.0
Soybean meal (47.5%)	14.5	14.5	14.5	14.5
Tallow	2.5	2.5	2.5	2.5
Sunflower oil	2.5	2.5	2.5	2.5
Salt (iodinated)	0.30	0.45	0.60	0.75
Biophos[2]	1.6	1.6	1.6	1.6
Limestone	1.6	1.6	1.6	1.6
Vitamin-mineral premix[2]	1.0	1.0	1.0	1.0
	100.0	100.0	100.0	100.0
Sodium content (%)[3]	0.16	0.22	0.28	0.34

[1] All diets were formulated to be iso-caloric and iso-nitrogenous with a c/p ratio of 151.

[2] See Table 23.

[3] Calculated values based on the analyzed sodium contents of each ingredient.

Table 25. Performance of young SCWL cockerels fed rye diets containing different levels of salt (Experiment 3 - Trial 1)[1]

Diet treatments	Body weight gain[2] (g/bird)	Feed intake[2] (g/bird)	Feed/gain
0.3% salt rye diet	65.9±3.37[c]	172.1±6.04[c]	2.62±.006[a]
0.6% salt rye diet	83.4±1.20[b]	202.9±2.02[ab]	2.43±.031[b]
0.9% salt rye diet	83.6±2.27[b]	196.8±3.43[b]	2.36±.039[b]
0.3% salt corn diet	102.1±2.64[a]	212.8±4.07[a]	2.09±.025[c]

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[1] $\bar{X}$ ± S.E. (Means within a column with a common superscript are not significantly different at 5% level).

[2] From day 6 to day 19.

diet was increased from 0.3% to 0.6% body weight gain and feed intake increased significantly. In addition, feed conversion efficiency was improved significantly by the increased salt level. There were no significant differences in growth rate, feed intake or feed/gain ratio between the 0.60% salt-rye and 0.9% salt-rye diets indicating that the improvement in performance of rye-fed birds by increasing the salt level reached a plateau at 0.6% dietary salt. When cockerels were fed a corn diet containing 0.3% dietary salt, the birds grew significantly faster and showed significantly better feed conversion efficiency than did cockerels fed the rye diets.

Relative body weight gain data were calculated using the 0.6% salt-rye diet as a reference point. The average body weight gain of birds fed the 0.3% salt-rye diet was calculated to be 79.0% of that of birds fed the 0.6% salt-rye diet. On the other hand, the average body weight gain of corn-fed birds was found to be 122.4% of that of birds fed the 0.6% salt-rye diet.

II. Trial 2

Performance data from young broiler chickens in Trial 2 are shown in Table 26. When the dietary salt level was increased from 0.3% to 0.4%, the growth rate improved significantly among birds fed rye diets. The growth rate tended to improve further when the salt level was increased up to 0.6%, however, the differences were not significant. Unlike the data from Trial 1 (Table 25), a significant improvement in feed conversion efficiency by increasing the salt level in the rye diets was not apparent although a trend was evident as the values decreased steadily with each increment in dietary salt. Corn-fed broilers showed

Table 26. Performance of broiler chickens fed rye diets containing different levels of salt (Experiment 3 - Trial 2)[1]

Dietary treatments	Body weight gain[2] (g/bird)	Feed intake[2] (g/bird)	Feed/gain
0.3% salt rye diet	117.5 ± 1.89^c	240.1 ± 1.35^b	$2.05 \pm .043^a$
0.4% salt rye diet	135.6 ± 7.47^b	263.7 ± 6.75^a	$1.96 \pm .112^a$
0.5% salt rye diet	146.7 ± 3.41^b	281.0 ± 7.32^a	$1.92 \pm .065^a$
0.6% salt rye diet	151.2 ± 4.87^b	272.1 ± 3.42^a	$1.81 \pm .072^a$
0.3% salt corn diet	184.2 ± 0.80^a	278.8 ± 2.31^a	$1.52 \pm .014^b$

[1] $\bar{X}$ ± S.E. (Means within a column with a common superscript are not significantly different at 5% level).

[2] From day 4 to day 13.

the best growth performance. The average body weight gain data of birds fed the 0.30% salt-rye and 0.30% salt-corn diets were 77.7% and 121.8%, respectively, of that of birds fed the 0.60% salt-rye diet.

III. Trial 3

Performance data of broiler chickens reared under practical field conditions and fed rye based diets varying in salt content are summarized in Table 27. No significant differences either in growth rate or feed conversion efficiency were found among the dietary treatments when birds were fed broiler starter diets. In addition, the birds showed remarkably poor feed conversion efficiency. When switched to finisher diets, however, the birds showed significant improvements in both growth rate and feed efficiency in response to increased dietary salt levels. As was the case for the birds housed in battery cages the improved performance for the floor-reared birds reached a plateau at the 0.6% dietary salt level. This trend was also apparent when the performance data for the overall 4-week feeding period was calculated as shown in Table 27. It is of interest to note that the values for feed conversion efficiency in broilers fed finisher diets were superior to those for the birds fed starter diets.

DISCUSSION

Results of all three feeding trials in Experiment 3 strongly indicate that the dietary salt level should be increased at least up to a level of 0.6% when growing chickens are fed diets based on rye. As shown in Figure 2, the relative growth rate of young chickens fed rye diets increased gradually up to 0.6% dietary salt supplementation and leveled off thereafter. Corn-fed birds, however, always showed significantly better growth and feed conversion efficiency than did chickens

Table 27. Performance of broiler chickens fed rye diets containing different levels of salt in a field condition (Experiment 3 - Trial 3)[1,2]

Periods	Dietary treatments	B.W. gain (g/bird)	Feed/gain
Starter (d 20-33)	0.30% salt	178±6.2	4.77±.259
	0.45% salt	226±30.4	4.24±.526
	0.60% salt	227±25.1	4.12±.410
	0.75% salt	227±6.3	4.12±.180
Finisher (d 34-47)	0.30% salt	567 ± 3.2^b	$2.84 \pm .068^a$
	0.45% salt	595 ± 25.7^b	$2.69 \pm .098^{ab}$
	0.60% salt	644 ± 3.5^a	$2.55 \pm .027^b$
	0.75% salt	645 ± 6.5^a	$2.51 \pm .033^b$
Overall (d 20-47)	0.30% salt	745 ± 7.6^b	$3.27 \pm .070^a$
	0.45% salt	821 ± 37.4^a	$3.06 \pm .084^{ab}$
	0.60% salt	871 ± 26.1^a	$2.94 \pm .096^b$
	0.75% salt	872 ± 12.7^a	$2.93 \pm .066^b$

[1] $\bar{X}$ ± S.E. (Means within a column with a common superscript are not significantly different at 5% level).

[2] Initial average body weights of each treatment were as follows (g/bird): 0.30% salt, 427; 0.45% salt, 429; 0.60% salt, 428 and 0.75% salt, 429.

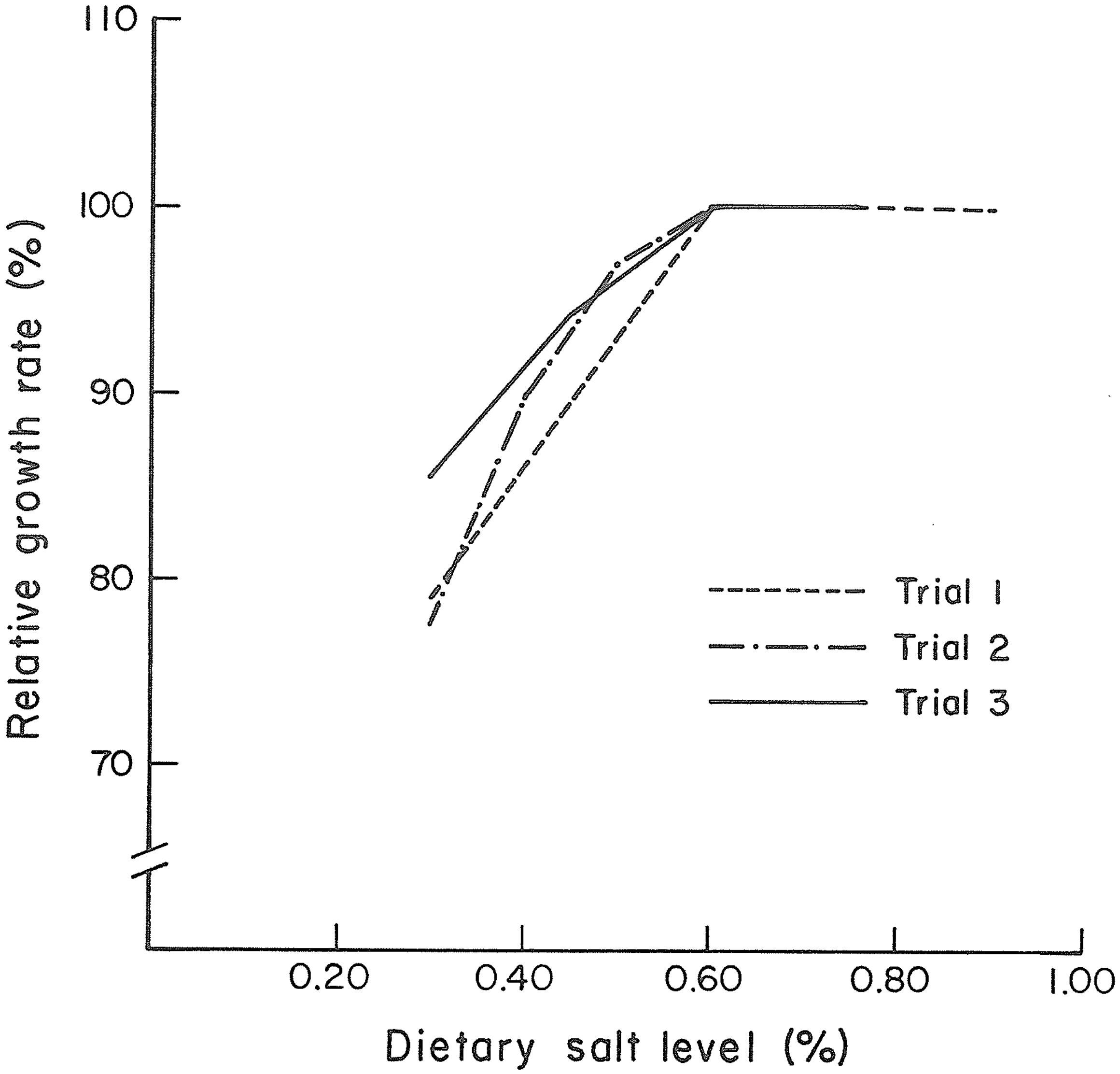

Figure 2. Relative growth rate of growing chickens fed rye diets containing varied salt levels (0.60% salt = 100%).

fed rye diets regardless of dietary salt levels.

The minimum salt requirement of poultry for optimum growth and production is subject to considerable variation. According to NRC (1977), the requirements of sodium and chloride for young chickens were 0.15% and 0.08%, respectively. The results of Experiment 3, however, indicate that the minimum sodium requirement for growing chickens fed a rye-based diet lies between 0.26 and 0.28%. Almost three decades ago, Slinger _et al_. (1950) reported that the salt requirement of growing chickens increased drastically (8 to 10-fold) when low fiber-high energy grains were replaced by high fiber-low energy grains, wheat by-products or cellulose. The findings of these researchers are in agreement with the results of this experiment since rye can be considered to be a high fiber-low energy grain.

The poor growth rate and impaired feed utilization in chicks fed rye diets containing 0.3% dietary salt in this experiment are only a few examples among many sodium deficiency symptoms described by Scott _et al_. (1976). The utilization of protein was also found to be affected in sodium deficient animals. Parthasarathy (1950) reported that the addition of 0.5% salt to the laying hen diet improved the utilization of the dietary nitrogen. Orent-Keiles and McCollum (1940) found that rats deficient in sodium did not have the ability to utilize protein as efficiently as did controls. It appears that not only protein utilization but also energy utilization is affected in sodium deficient animals. This is because sodium plays an essential role in the processes leading to the absorption of sugars and amino acids in the intestine as reviewed by Curran (1965) and Crane (1965). However, it is not clear whether the poor performance of sodium-deficient chicks caused by feeding 0.3% salt-rye diets in the current experiment was due to the inhibited absorption of sugars and amino acids, or due to other factors including the types of physiological changes observed in Experiment 2.

The results of Experiment 2 clearly showed that the major route of sodium excretion in rye-fed birds is via feces, while the urine is the major excretory pathway of sodium in corn-fed birds. This observation confirms the earlier findings of Koike _et al_. (1964). The fact that birds fed diets high in dietary fiber increase the salt requirement (Slinger _et al_., 1950) by modifying the major route of sodium excretion (Koike _et al_., 1964) leads to the conclusion that the dietary fiber present in rye inhibits the sodium absorption in the gut. Owing to the resistance to digestive enzymes and its bulkiness, the dietary fiber increases the total weight and bulk of digesta in the gut. Therefore, the sodium ions present in that digesta would have less chance to contact with absorptive epithelium and hence less chance to be absorbed. More research is needed to elucidate the mechanism(s) of salt deficiency symptoms in rye-fed chickens in this respect.

SUMMARY

A series of feeding trials were conducted with young broilers and cockerels to determine if salt, per se, was a contributing factor in the growth-depressing properties of rye. Growth rate and feed conversion efficiency in young chickens improved significantly when the dietary salt level increased from 0.3% to 0.6% in rye-based diets, but not to a level equivalent to that of corn-fed birds. The relative growth rate of chickens fed 0.3% salt-rye diets was 78-86% of that of birds fed a

0.6% salt-rye diet. The cause of salt or sodium deficiency in rye-fed birds was briefly discussed.

GENERAL CONCLUSIONS

1. Water and salt metabolism of the chicken is influenced by the type of dietary grain and by dietary salt level.
2. Rye-fed chickens are more resistant to excessive intake of salt than are corn-fed birds. When low levels of salt are fed, rye-fed chickens are more sensitive to salt deficiency than are corn-fed birds. This characteristic of rye is attributed to a high concentration of dietary fiber.
3. When chickens are fed diets high in dietary fiber, sodium is excreted mainly via feces. When fed diets low in dietary fiber, urine is the major excretory pathway of sodium.
4. Dietary fiber increases fecal sodium excretion by reducing the absorption of sodium from the gut. Two properties of dietary fiber appear to be responsible for this phenomenon. Firstly, dietary fiber increases fecal weight, and secondly, it decreases fecal bulk density (g/mℓ). These characteristics of dietary fiber render sodium ions less chance for contact with the absorptive epithelial cells and therefore reduce sodium ion absorbability, especially in the lower gut.
5. Experimental evidence indicates that the freeze-dried water extract of rye inhibits the sodium absorption in the gut when fed to chickens by mechanism(s) different from that of dietary fiber.
6. Complete removal of the substance(s) that causes reduced sodium absorption in the gut is not brought about by the water extraction process. However, it was possible to eliminate the sticky and/or

watery droppings phenomenon associated with the feeding of rye to poultry by this process.

7. The sticky and/or watery droppings phenomenon associated with the feeding of rye was not eliminated by increasing dietary salt level. There is a possibility, however, to reduce the extent of this problem by increasing dietary salt level to a point where diuresis would not ensue in intact birds fed rye.
8. Indirect evidence indicates that the large intestine, not the cloaca, is the major site of post-renal modification of urine which is important for the normal salt and water economy of the chicken. Colostomized birds, therefore, tend to require more salt to maintain homeostasis.
9. The growth performance of young chickens fed diets based on rye can be improved significantly by increasing the dietary salt level from 0.3% up to 0.6% where the improvement reaches a plateau.

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