# SALT TOLERANCE AND SALT PREFERENCE IN THE JAPANESE QUAIL AS A FUNCTION OF PRIOR EXPERIENCE DRINKING NACL SOLUTIONS

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# CHAPTER I

# INTRODUCTION

## What Is Stress?

"Stress is the state manifested by a specific syndrome which consists of all the nonspecifically induced changes within a biological system" (Selye, 1956, pp. 54). Further, stress is a hypothetical construct that is useful only to the extent that it can help organize unrelated findings and result in a more parsimonious explanation of empirical findings. The above definition of stress as given by Selye states that stress is a syndrome that is identified by certain visible manifestations, and although stress is identified by a specific syndrome, it is nonspecifically induced. Heat, cold, thirst, hunger, pain, and many other different stress inducers can result in the same specific syndrome of stress. The stress syndrome is the sum of those changes in an organism that are nonspecifically induced. Although differing considerably in their effects on an organism, heat, cold, thirst, hunger and pain can all be called stressors, because they all elicit a specific, identifiable syndrome in the organism.

One of the major changes that occurs as a result of stress is the increase or decrease in the hormonal activity of the adrenal glands. The level of activity of the adrenal glands is very indicative of the stress syndrome, and can actually be used to identify different stages in the stress syndrome. For example, continued exposure to very cold temperatures first results in the adrenal cortex discharging all its supply of microscopic fat granules containing the adaptive cortical hormones. This stage is called the alarm reaction. If the stress is not too intense, the adrenals will be overactive and become laden with an excess of fat droplets. This comprises the stage of resistance. The eventual loss of the excess fat droplets results in the stage of exhaustion. Selye (1956, pp. 87) showed this diagramatically as follows:

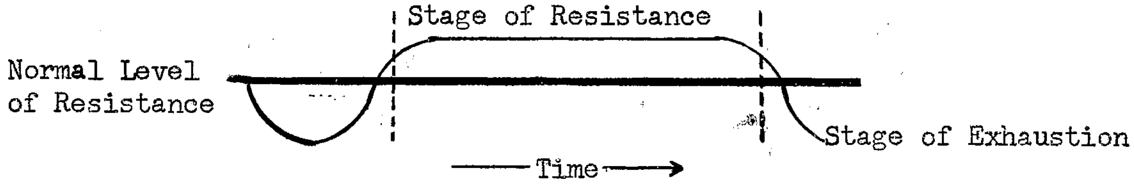

Figure 1. Diagram of GAS.

An excellent experimental demonstration of the above figure is given by Selye (1956, pp. 88-89). One hundred rats were placed in a freezer. The alarm reaction was regarded as occurring during the first 48 hours since the rats were found to have large fat-free adrenals. After 48 hours, 20 rats were placed in an even colder chamber together with a control group that had not been in the original freezer. With resistance measured in terms of survival, the group that had already developed an alarm reaction was found to be less resistant than normal. After another five weeks, a second sample was taken from the original, moderately cold freezer. The subjects were then fully adapted to the cold environment and upon being placed in the colder chamber were found to be more resistant than normal (control Ss). This corresponded to the stage of resistance. Interestingly, the resistance was not permanent, for after several months in the cold, the rats could not survive even in the moderately cold freezer, which indicated the final stage of exhaustion. According to Selye, "Adaptability can be well trained to serve a special purpose, but eventually it runs out; its amount is finite" (Selye, 1956, pp. 88). He pointed out that a similar pattern has been found with forms of stress other than cold, thus leading to his concept of "adaptation energy." Since a finite amount of adaptation energy exists in an organism, it is interesting to consider the possibility that adaptation to one stressful situation may be at the expense of being able to adapt to future stress. Selye considered stress to be the rate of wear and tear on the body; he felt that death does not occur as a result of old age, but as a result of certain parts of the body wearing out.

There are two major types of hormones secreted by the adrenal cortex, the proinflammatory (P-C) and the anti-inflammatory (A-C) corticoids. The P-C's promote the formation of inflammation in the body, an adaptive response, and influence mineral metabolism by causing the retention of sodium and excretion of potassium. P-C's are also called mineralocorticoids. The A-C's, as the name implies, inhibit the formation of inflammation in the body.

Inflammation is generally identified by reddening, heat, swelling, and pain in the body of an organism. It is an adaptive response that represents an active defense reaction in that it forms a barricade around the invaded territory demarcating the sick from the healthy. Several disadvantages are associated with the formation of inflammation; the most critical of these is that the rapidly proliferating tissue may interfer with the function performed by the inflamed area.

The adaptive hormones (P-C's) may or may not provide the most appropriate response to an irritant. The formation of inflammation is generally quite adaptive where certain infections are concerned, but the body may overreact to less harmful irritants, resulting in a situation in which over-adaptation actually comprises the disease. Hay fever is a good example of an overly adaptive response resulting in a disease of adaptation.

Both A-C's and P-C's have drastic effects on the kidneys, which are known to play a major role in maintaining the body's equilibrium during general adaptation to stress. The kidneys regulate the composition of the blood and tissue and also adjust blood pressure; both of these functions are critical in maintaining life. The actual mechanism of blood pressure regulation is little understood, but it is known that partial constriction of the renal arteries results in an excess of renal pressor substances (RPS) excreted into the blood. Although the exact mechanism is not known, the corticoids, especially the P-C's, can produce certain inflammatory arterial lesions which constrict the blood vessels of the kidneys. This results in an increase in RPS, which causes constriction in the peripheral blood vessels throughout the body which, in turn, increases the resistance against which the heart pumps, thus raising the blood pressure. Large amounts of P-C's result in a kidney disease called nephrosclerosis, or Bright's Disease, which is accompanied by a marked rise in blood pressure and inflammatory changes in the walls of the arteries throughout the body.

The stimulators of the P-C hormones, or mineralocorticoids, are not known, although it is fairly certain that minerals in the blood (sodium and potassium) can act on the adrenals to regulate the mineralocorticoids in accordance with the requirements of the body. The amount of salt in the diet of an organism can be a critical factor in determining the results of the presence of P-C hormones in the body. Selye (1956, pp. 129-133) demonstrated that increased salt intake was sufficient cause for an otherwise harmless injection of DOCA (P-C hormone) to eventuate in thirst, edema, dropsy, and a rise in blood pressure along with renal, cardial and arterial changes that were identical to the symptoms of Bright's Disease.

The nature of adaptation was of prime importance to Selye's theory of the General-Adaptation-Syndrome (GAS). The GAS consists of the sum of the nonspecific responses to continued stress across time and encompasses the three stages mentioned above. The stages can be viewed as different phases in the development of an adaptive reaction. "An essential feature of adaptation is the delimitation of stress to the smallest area capable of meeting the requirements of a situation" (Selye, 1956, pp. 120). Adaptation always represents a spacial concentration of effort. The alarm reaction can be viewed as an auxiliary mechanism which is mobolized to maintain life since no particular "organ-system" has as yet been specifically developed to cope with the task at hand. The second stage, that of resistance, is entered into when adaptation is acquired due to the development of the most appropriate channel of defense. As wear and tear occurs in the most appropriate channels of defense, the organism becomes exhausted and dies.

This is the stage of exhaustion (Selye, 1956, pp. 87-89).

The response of an organism to a particular level of stress can be altered, in part, by prior conditions that may in some way alter the stage of the organism's adaptation to the initial exposure to stress. If an organism is in the stage of resistance and already has its most appropriate channels of defense developed, it will probably show superior resistance to stress; if the organism is already in the stage of exhaustion, its response to the stress will probably be ineffective.

The study of stress and stress inducers is, by itself, quite important, but the continual adaptation and conditioning to stress that naturally occur in the body throughout an organism's life have not received the emphasis they deserve. Stress exists only as its manifestation in a biological system, and is important only in terms of how the biological system responds to it. "Adaptability is probably the most distinctive characteristic of life" (Selye, 1956, pp. 118).

## CHAPTER II

## REVIEW OF THE LITERATURE AND STATEMENT OF THE PROBLEM

Given the above background information concerning the analysis of stress, what can be said about the results of excess NaCl intake and its relation to stress?

### Effects of Excess NaCl Intake

Selye (1943) demonstrated that the DOCA induced Bright's Disease syndrome could be produced in chicks by giving salt water as the only source of drinking water. A 2% NaCl solution was toxic enough to produce 100% deaths in a two-day-old chicks. A 0.90% NaCl solution resulted in a more chronic course when it was given to 19-day-old chicks. The chicks increased their intake and exhibited a state of edema that is identified by an excess retention of water in the body. The 19-day-old 0.90% group, some of which survived for 20 days, exhibited a decrease in edema between days 10 and 20 and entered into the second stage of the disease with increasing development of nephrosclerotic changes identified by cardiac hypertrophy and renal constriction. An additional group of 4-week-old chicks was given a 0.30% NaCl solution instead of drinking water. The weak NaCl solution had no toxic effect on the 28-day-old chicks. Thus, a 0.90% NaCl solution (approximately isotonic) was capable of causing drastic behavioral (accelerated intake) changes as well as physiological changes (nephrosclerosis and disturbance in water balance).

The 19-day-old chicks given the 0.90% NaCl solution exhibited a syndrome that can be separated into the various stages of the General Adaptation Syndrome. The presence of the alarm reaction is substantiated by an initial exaggerated reaction to the NaCl solution. The chicks greatly increased their water intake, became edemic, and their kidneys became enlarged. Across days the kidneys appeared to become specialized or adapted to dealing with the stress of the NaCl load. Life was maintained in the meantime by exaggerated NaCl solution intake and the appearance of an edemic state. This can be regarded as an auxiliary mechanism to help maintain life while some organ-system undergoes development to cope with the stress. By days 10 to 20 the birds presumably had entered or were entering the stage of resistance. The edemic symptoms disappeared, the kidneys showed various changes in the tubular walls, and cardiac hypertrophy appeared. This provides a good example of how adaptation is a spacial concentration of effort in the development of the most appropriate specific channel of defense. Since the kidneys regulate osmotic pressure of body fluids, total volume of water in the body, and distribution between intracellular and extracellular portions (Robinson, 1964), they are the most appropriate and specific channel of defense against salt-poisoning. Selye (1943) did not determine whether the above physiological changes resulted indirectly from the salt acting upon the corticoid activity of the adrenal glands or from salt acting directly on the kidneys. Research (Wilgram & Ingle, 1961), to be reviewed later, indicates the latter is probably the case.

Krakower and Goeltsch (1945) documented the occurrence of anasarca, an edemic-like state, in 3-week-old chicks given a 0.90% NaCl solution to drink with additional salt in the food. Fluid intakes were observed to range from 50% to 100% of body weight per day. The high liquid intake was believed to be responsible for edema and other changes. Krakower and Goeltsch also reported concurrent changes such as cardiac hypertrophy and marked renal glomerular enlargement, with the formation of new loops and lobules in the chicks.

NaCl concentrations of 0.50% to 1.00% in drinking water, or 1.00% to 3.00% added to mash, produced typical edema and ascites, a collection of serious fluid in the cavity of the abdomen, in five to eight-day-old turkeys (Scrivner, 1946). Krakower and Heino (1947) reported that, for chicks, a daily salt load must exceed 0.30 gm/100 gm of body weight if morphologic changes in heart and kidneys are to take place. Renal hypertrophy, mostly tubular mass, was variable but appeared to increase in direct proportion to increases in the daily load of NaCl. Marked hypertrophy of renal arteries and preglomerular arterioles was a consistent finding in birds with a high salt intake. Blood pressure appeared higher in salt groups. Krakower and Heino concluded that the higher blood pressure in salt groups was probably more a result, rather than a cause, of cardiac and arterial hypertrophy.

The effect of excess salt intake on blood pressure has been studied by other researchers. Lenel and Rodbard (1948) reported that blood pressure in 6-week-old chickens rose when 0.90% and 1.20% saline solutions were substituted for drinking water; the degree of hypertension appeared to depend on the concentration of the salt water ingested. Hyperplasia and proliferation of glomerular tufts and Bowman's capsule with compression of the capillaries were found after prolonged periods of drinking salt water. Dahl and Heine (1961) found the amount of hypertension induced in chicks from feeding an excess of "sea salt" resulted in significantly higher blood pressure than an excess of NaCl alone. Sea water is generally found to be more toxic than similar NaCl solutions. Sapirstein, et al. (1950) induced hypertension (higher blood pressure) in rats by watering them with a 2.00% hypertonic NaCl solution. The hypertension developed only after a latent period of 1-4 weeks of consuming the hypertonic NaCl solution. Hypertrophy of the heart and kidneys relative to body weight was present at autopsy. Meneely, et al. (1953) studied the effects of varying percentages of NaCl in the food on rats. Water was given *ad libitum* and NaCl in the food was varied from 0.01% to 9.80%. Hypertension was produced by the high salt diet in 9 months. Since water was given *ad libitum*, the rats could probably reduce some of the effects of excess salt by diluting the load with hypotonic water. A syndrome of edema and renal failure was more clearly observed in the higher percent NaCl groups. Significant histologic changes were also reported to be present, especially in the kidneys of the higher percent NaCl groups. Koletsky (1958) reported that with a 1.00% NaCl solution for drinking water, a period of several months of the regime was usually required to produce both elevated blood pressure and vascular lesions in rats. The elevated blood pressure can occur before there are any significant renal lesions. Koletsky reported that the mechanism of salt injury is unknown, although it is possibly related to retention and intracellular accumulation of Na, which results in a critical electrolytic imbalance. Once hypertension has been induced in rats by feeding of excess salts, it may become self-sustaining (Dahl, 1961). Dahl reported that after chronic feeding of sodium salts for 12 to 13 months, withdrawal of the salts from the diet failed to result in any significant drop in blood pressure for about two-thirds of the rats tested. Further research indicated adrenal glands were found unnecessary to induce hypertension in rats with excess salt in the diet (Wilgram and Ingle, 1961). Adrenalectomized rats given excess salt developed increased heart weight, lesions in the kidneys, and hypertension. Wilgram and Ingle concluded that the mineralosteroids of the adrenal cortex are not the primary pathogenic agents in inducing these conditions, but may merely potentiate the primary damaging effects of high salt intakes by promoting sodium retention. Also, hypertension was induced in dogs by Vogel (1966) by increasing the dietary intakes of NaCl to 2 gm/kg body weight/day and providing a 0.90% NaCl solution for drinking water. Blood pressure reportedly increased 55% over a period of 26 days. In summary, excess salt feeding appears capable of consistently inducing hypertension in an organism. The mechanism is not specifically known, but salt can induce changes somewhat independent of the corticoid activity of the adrenal glands (Wilgram & Ingle, 1961) and an electrolyte imbalance mechanism was suggested by Koletsky (1958). The morphological changes and the extent of damage caused by excess salt varies according to concentration of NaCl presented, type of organism, length of time of presentating, presence or absence of hypotonic solutions, and prior alternations in the organism, such as adrenalectomy, that alter the response of the organism to salt.

Several related studies to be reviewed have been less concerned with hypertension and other physiological changes associated with excess salt intake. The main problem investigated by these studies was the response of the organism to NaCl solutions as measured by tolerance tests and liquid intake tests. Results from studies of terrestrial birds are emphasized. Mourning doves exhibited an accelerated liquid intake when 0.15m NaCl was present, but increasing the concentration to 0.25m NaCl resulted in a sharp decline in intake (Bartholomew and MacMillen, 1960). House finches (Carpodocus mexicanus) showed an increase in liquid intake with increase in salinity up to 0.30m NaCl; however, they became erratic at 0.40m and decreased intake at 0.50m NaCl (Bartholomew and Code, 1958). These birds were able to maintain body weight while drinking concentrations up to 0.25m NaCl. Molarities up to 0.40m could extend survival beyond that found for complete water deprivation. California quail (Laphartyx californicus) did not always show increased liquid intake when hypertonic NaCl was present. Rather, they maintained a uniform level of consumption for salt concentrations up to about 75% sea water, which is approximately 040m NaCl (Bartholomew and MacMillen, 1961). California quail could tolerate NaCl concentrations as high as 37.5% sea water.

The liquid intake and body weight of various subspecies of Savannah sparrows (Passerculus sandwichensis) has been studied by Cade and Bartholomew (1959). The subspecies brooksi was found to increase liquid intake with increasing concentrations of NaCl up to 0.40m, with body weight holding constant. Both liquid intake and body weight decreased sharply when a 0.60m NaCl solution was present; some birds did not survive the high concentration. The subspecies beldingi showed a decrease in liquid consumption with increasing salinity and was able to maintain body weight on a 0.55m NaCl solution. A pattern similar to the beldingi was exhibited by a third subspecies, rostratus. Poulson and Bartholomew (1962) have extended the research on the beldingi and brooksi. Measures of osmotic pressure and chloride concentration in serum and urine indicated that both subspecies increased urine chloride concentration and urine osmotic pressure with increasing NaCl concentration of the drinking solution.

Harriman (1966a) determined the salt tolerance and liquid intakes for starlings (Sturnus v. vulgaris) and purple grackles (Quiscalus q. quiscula). Both starlings and purple grackles showed elevated fluid intakes when 0.20m NaCl was present, but decreased fluid intakes at higher concentrations. On a 10 day survival test with 0.25m NaCl as the drinking water starlings were found to have 100% fatalities and the purple grackles had 100% fatalities at 0.35m NaCl.

## Adaptation to the Stress of Excess Salt

Selye (1956, pp. 118-124) pointed out the possibility of adaptation factors in stress. Internal factors, such as heredity and past experiences, may leave permanent changes in the body and in the responses of the organism to stress. External factors, such as diet, may adapt an organism to stress without permanently altering its body (Selye, 1956, pp. 95-98). Internal and external adaptation may increase resistance, decrease resistance, or have no effect on the resistance to a particular level of stress; these shall be designated as positive, negative or neutral adaptation, respectively. The example given earlier in the review of the rats in a deep freeze is an example of positive adaptation; that is, increased resistance to stress (after five weeks). Salt in the diet of an animal can result in a decrease in resistance, or negative adaptation, to the stress of DOC injections (Selye, 1956, pp.

128-138). The question this review is concerned with is whether an organism can be adapted to the stress of hypertonic NaCl solutions. Few studies have dealt with this problem explicitly, but several studies supply relevant data. For example, Bartholomew and MacMillen (1961) found that normally hydrated California quail lost weight when given solutions more concentrated than 37.5% sea water; yet, when subjected to dehydration, they could utilize much higher concentrations of sea water and regain their weight. Dehydration served as an adapting factor that increased the quails' resistance to stress as measured by weight loss. Cade and Bartholomew (1959) reported that for a single member of the subspecies (rostratus), which was subjected to water withdrawal, "Its capacity to resist dehydration was apparently related to the salinity of water on which it had been subsisting immediately prior to the dehydration test. The more saline the water it had been drinking, the better it maintained its weight after withdrawal of water" (Cade and Bartholomew, 1959). The amount of adaptation that took place was believed by the authors to be a function of the concentration of NaCl the bird had been drinking. In this case, the resistance to stress was increased by, and was a function of, the salt water concentration on which the bird had previously been subsisting. This also provides an example of a stress-inducer of one kind (hypertonic NaCl) serving as an adapting factor for another kind of stress-inducer (water deprivation). The period of positive conditioning or adaptation can be best regarded as the time interval during which an organism is developing its most efficient means of dealing with a particular kind of stress and pre-adapts itself for Selye's "stage of resistance." Whether a particular event or set of stimuli acts as a positive, negative or neutral adapting factor for subsequent stress must be determined empirically. The generality and specificity of the effects of various positive, negative, or neutral adapting factors on different kinds of stress-inducers have not yet been fully explored.

Nasal salt glands in domestic ducks have been shown to increase in relative weight as a function of the salt concentration the birds had been adapted to drinking (Ellis, et al., 1963, Schmidt-Nielson and Kim, 1964). Schmidt-Nielson and Kim (1964) also showed that salt-adapted ducks were better adapted to dealing with the excess NaCl incurred by intravenous NaCl injections. The adapted ducks could excrete more of the salt load and at a more rapid rate than the nonadapted ducks which were raised on fresh water. Prior experience with hypertonic saline solutions resulted in permanent alterations in the adapted ducks' nasal glands. The increased efficiency and size of the nasal glands served to preadapt the ducks to later, more stressful salt loads.

Only one other study has been concerned with the possibility of increasing the salt tolerance of an organism by preadaptation. Jelînek, et al. (1966) gave rats, aged 16, 33, and 86 days a 2% NaCl solution for drinking water for 70 days. They reported that salt-adapted groups could excrete a urine higher in sodium and urea concentrations in response to a hypertonic salt load than could the nonadapted control groups. Age was found to be an important factor in determining how well the rats could be adapted to the 2% conditioning solution. The 16-day-old group was the group least capable of adapting to the 2% hypertonic salt solution and often drank large amounts of water, lost weight and died. All groups were reported to show both an absolute and relative to body weight increase in kidney weight, but increased kidney size and increased renal concentration ability were not consistently related.

Generalizing from the above studies, it appears that subjecting an organism to the proper amount of stress (hypertonic solutions or water deprivation) can serve as an adapting factor that may preadapt an organism so that it can more efficiently deal with particular kinds and more intense forms of stress. The above paradigm of adaptation to stress is similar to the example of Selye's rats in a deep freeze (Selye, 1956). Of the number of stress-inducers investigated, only a few have considered adapting factors (Selye, 1956). With the known importance of sodium in the maintenance of life, it is surprising that so few studies have in any way related an organism's response to NaCl to any preadapting factors that might drastically alter the organism's usual response to salt.

## Salt Preference as a Function of Hypertension and Other Variables

Only new stimuli presented to an organism may cause physiological and/or behavioral changes that comprise the process called adaptation. One of the major behavioral measures associated with the research on salt is the preference or aversion an organism displays for various salt concentrations. The term preference (aversion) implies a choice (Young, 1955), and the subject is generally given a standard solution which is paired with various comparison solutions. The preferred (less aversive) solution is the one that results in the greater relative intake of the two test solutions. Under certain conditions, it seems reasonable that these behavioral conditions should somehow complement physiological conditions that exist in the organism. That is, physiological indices should have their behavioral correlates. For example, if an organism is offered two solutions, one of which is so hypertonic it causes edema and perhaps death and the other of which is pure water, it would be considered adaptive if the organism chose the less hypertonic solution. What, then, is the relationship between an organism's preference (or aversion) for NaCl solutions and various physiological states that exist in the organism? This review will be limited to those physiological states that can be induced by, or related to, excess NaCl intake.

Abrams, et al. (1949) studied the effects of hypertension in rats on self-selection of salt solutions. The kidneys were encapulated in latex sheaths and the subjects were fed .17m NaCl solutions making the rats hypertensive. The hypertensive group consistently took less NaCl than normal rats.

Fregly (1955) bilaterally encapsuled the kidneys of rats with latex envelopes. The rats were in two groups, one 10 weeks, the other 20 weeks old. Both groups developed a significant rise in blood pressures within 2-4 weeks. The rise in blood pressure was accompanied by a rise in water intake. Water and a 0.15m NaCl solution were simultaneously present throughout the experiment. The intake data revealed a relative aversion to NaCl in the young hypertensive rats eight weeks after the operation, during which time the young group's blood pressure was at its highest point. The older group developed maximal blood pressure nine weeks after the operation, but failed to display any consistent NaCl aversion. The life span of the younger, hypertensive rats were reported to be significantly shorter than the appropriate control group; the older hypertensive rats were not affected. In a later study

Fregly (1956) determined the effects of hypertension, induced as above, on the preference threshold determined by a two-bottle preference test. Distilled water was the standard solution and varying concentrations of NaCl solution served as the comparison solution. Preference thresholds for normal and hypertensive rats were the same between .008 and .016m NaCl. A relative NaCl aversion was reported in the hypertensive rats when the NaCl comparison solution was .09m or greater. The normal rats continued to show a preference for the NaCl solutions at concentrations above .09m. Fregly (1959) wanted to determine whether the aversion to NaCl displayed by hypertensive rats was specific to NaCl, or if such an aversion would also exist for other sodium solutions. Thus, identical preference tests were carried out with KCl, $Na_2SO_4$, LiCl and sodium saccharin. A similar aversion pattern was found for these compounds as had been found to exist for NaCl. The nonhypertensive control group did not display the increased aversion. Fregly concluded that the NaCl aversion manifested by hypertensive rats was not specific, but part of a general salt aversion. Fregly (1961) reported in a later study that if the sodium was presented in the food, hypertensive rats could not regulate their sodium intake.

Dahl, et al. (1962), taking a somewhat different approach, was able by selective inbreeding to produce two statistically significant populations from one unselected strain of rats that were different in terms of the resistance to the development of induced hypertension from a high salt diet. Wolf, et al. (1965), extending the approach of Dahl, et al. (1962), determined the voluntary NaCl intake for two populations of rats which differed in their susceptibility to salt induced hypertension. The hypertensive susceptible group ingested significantly less saline solution than the genetically hypertensive resistant group. Dehydroxycorticosterone (DOCA) nullified the differences between the two groups, but adrenalectomy had no effect on the differences. Wolf, et al. speculated that the aversion for saline solutions might be regarded as an early indicator of developing hypertension. Herxheimir and Woodbury (1960), investigating the effects of DOCA-treatment, demonstrated that DOCA-treated rats decreased their salt preference, while the untreated control group showed no decrease in preference. The possibility of genetic factors determining the susceptibility of an organism to salt induced hypertension represents a fruitful new approach that helps show the basic importance of salt in the life of an organism.

## Salt Preference in Terrestrial Birds

The final area to be reviewed concerns those studies that have been primarily concerned with determining the natural salt preferences (or aversions) associated with various species. Emphasis will be specifically on terrestrial birds.

In most species of terrestrial birds thus far investigated concentrations of NaCl, when paired with distilled or fresh water, have resulted in indifference or aversion to all NaCl solutions (Harriman, 1966b). Most mammals show an initial preference for NaCl concentrations up to approximately isotonic concentrations, followed by an increasing aversion as the NaCl solutions become increasingly hypertonic (Young, 1961). Since terrestrial birds show only indifference for very low NaCl concentrations instead of the mammalian preference, it is difficult to determine if birds are capable of discriminating among various low concentrations of NaCl. Therefore, a legitimate question to be considered is whether terrestrial birds are capable of discriminating between various NaCl solutions and distilled water at other than extremely hypertonic or toxic levels. Salt water discrimination tests given to mourning doves (Bartholomew and MacMillen, 1960) revealed that doves could only discriminate between a solution which they could not use to maintain water balance and a solution on which they could maintain a water balance. California quail (Bartholomew and MacMillen, 1961), unlike the mourning dove, can discriminate between salt solutions below the concentration (37.5% sea water) on which they can maintain body weight.

Research with starlings and purple grackles indicated that significant aversion does not occur until 0.15m NaCl concentration for starlings and 0.50m NaCl concentration for grackles (Harriman, 1966a). Starlings cannot survive on a 0.25m NaCl solution, while grackles cannot survive on a 0.35m NaCl solution (Harriman, 1966b). Starlings show aversion to NaCl solutions well within the maximum NaCl concentration they can tolerate, while grackles do not display significant NaCl aversion until the concentration is considerably above the level they can utilize. As pointed out by Harriman (1966a), tolerance and preference may or may not be interrelated in helping the organism adapt.

Preference tests have been conducted for bobwhite and Japanese quail, but only a single NaCl solution (2%) was used (Brindley, 1965). The 2% NaCl solution was found to be aversive by both species of quail.

The salt-preference data indicates that terrestrial birds show an indifference or aversion to all NaCl solutions. The concentration significantly rejected by a particular species may, or may not, be related to the maximum concentration the specie can tolerate. Few preference tests have clearly demonstrated whether terrestrial birds are capable of discriminating among more dilute NaCl solutions.

## Statement of the Problem

This study investigated the response of Japanese quail to NaCl solutions which were substituted for drinking water. One objective was to determine whether Japanese quail show the usual rise in liquid intake with rising salt concentration, and if the particular pattern of liquid intake is altered across time.

Salt tolerance and salt preference were investigated as functions of the concentration of NaCl to which the Japanese quail had been preadapted. The salt tolerance test determined whether prior experience with NaCl solutions could in any way result in greater tolerance for higher NaCl concentrations. The preference test provided information on whether previous experience or adaptation to NaCl solutions altered the subjects' future acceptance or rejection of a range of NaCl solutions. Also, the possible relation between salt tolerance and salt preference was investigated.

The above findings were related to Selye's theory of adaptation to stress.

Finally, the study provided empirical data on an excellent experimental subject, Japanese quail (Wetherbee, 1961). Little or no information is available regarding their water and salt balance.

# CHAPTER III

# METHOD

## Subjects

Fifty-five Japanese quail (Coturnix coturnix japonica), supplied by the Oklahoma State University Poultry Science Department, were fed *ad libitum* Purina Game Bird Startena. Room temperature was maintained between 71 and 79 degrees F., and the humidity varied between 61 and 71 percent.

## Apparatus

The salt preference tests were given in individual cages (16 x 13 x 24 in.). Individual cages (21 x 9 x 8 in.) were used for the salt tolerance test. All solutions were presented in glass drinkers with inverted pint jars. Liquid intakes were measured to the nearest 0.5 gm with a control drinker being used to determine evaporation.

## Preliminary Procedure

The subjects were randomly divided into three groups when they were 20 days old. During the adaptation schedule the Ss were cages with groups of four or five Ss to a cage (16 x 13 x 24 in.). Group I (18 Ss) was maintained on distilled water while Group II (19 Ss) and Group III (18 Ss) were gradually adapted to drinking 0.15m NaCl and 0.20m NaCl solutions, respectively. A salt-adaptation procedure similar to Ellis, et al. (1963) provided the following schedule for Group II and Group III:

TABLE I

ADAPTATION SCHEDULE FOR GROUP II AND GROUP III

| Group II (0.15m) | | | Group III (0.20m) | | |
|---|---|---|---|---|---|
| NaCl present | Distilled water | Days | NaCl present | Distilled water | Days |
| 12 hours | 12 hours | 5 | 12 hours | 12 hours | 5 |
| 16 hours | 8 hours | 5 | 16 hours | 8 hours | 5 |
| 20 hours | 4 hours | 20 | 20 hours | 4 hours | 20 |

Forty-nine Ss survived the adaptation schedule and resulted in 17, 16, and 16 Ss in Group I, Group II and Group III, respectively.

### Preference and Tolerance Test Procedure

Six Ss were randomly selected from each of the three groups and were subjected to a tolerance test. The remaining 31 Ss were given a two-bottle preference test.

Tolerance. The 18 Ss subjected to salt tolerance were individually caged and were given a 0.25m NaCl solution as the only available water supply with ad libitum access to food for 10 days. Body weights and liquid intakes were recorded every four hours until the first death occurred.

Preference. At the end of the 30-day preliminary adaptation schedule, 31 Ss were individually given 48-hour two-bottle preference test (positions altered every 24 hours). Double distilled, deionized water served as the standard solution and eight molarities of NaCl as the comparison solutions (0.10m, 0.15m, 0.20m, 0.25m, 0.35m, 0.50m, 0.75m, and 1.00m NaCl). Each S received an individually randomized order of presentation of the NaCl solutions until each was tested with all eight solutions.

# CHAPTER IV

# RESULTS

## Initial Weights

The mean body weights of the Ss at age 20 days were as follows: Group I, (57.66; SD = 4.49 gm); Group II, (57.34; SD = 7.04 gm); and Group III, (60.36; SD = 6.59 gm).

The mean body weights at the end of the preliminary schedule and start of the tolerance and preference tests were as follows: Group I, (117.94; SD = 14.90 gm); Group II, (106.50; SD = 13.56 gm); and Group III, (106.88; SD = 18.54 gm). The body weights during the tolerance test were plotted as mean percent of initial body weight.

## Adaptation

In Figure 2 the intakes of the test solutions (20-hour period) for the three groups are plotted as mean percent intake/100 gms body weight/daily 20-hour period for the last eight adaptation days. Each point represents a mean for four cages, and each cage contained four or five subjects. Total intake for each cage was divided by total cage gm body weight. The data were analyzed by means of a 3 x 8 factorially arranged analysis of variance with repeated measures (Table II).

Because the adaptation level (A) x blocks-days (B) interaction was significant, only the simple effects could be interpreted (Winer, 1962, pp. 174-178). The simple effects of adaptation level for Day 23 were

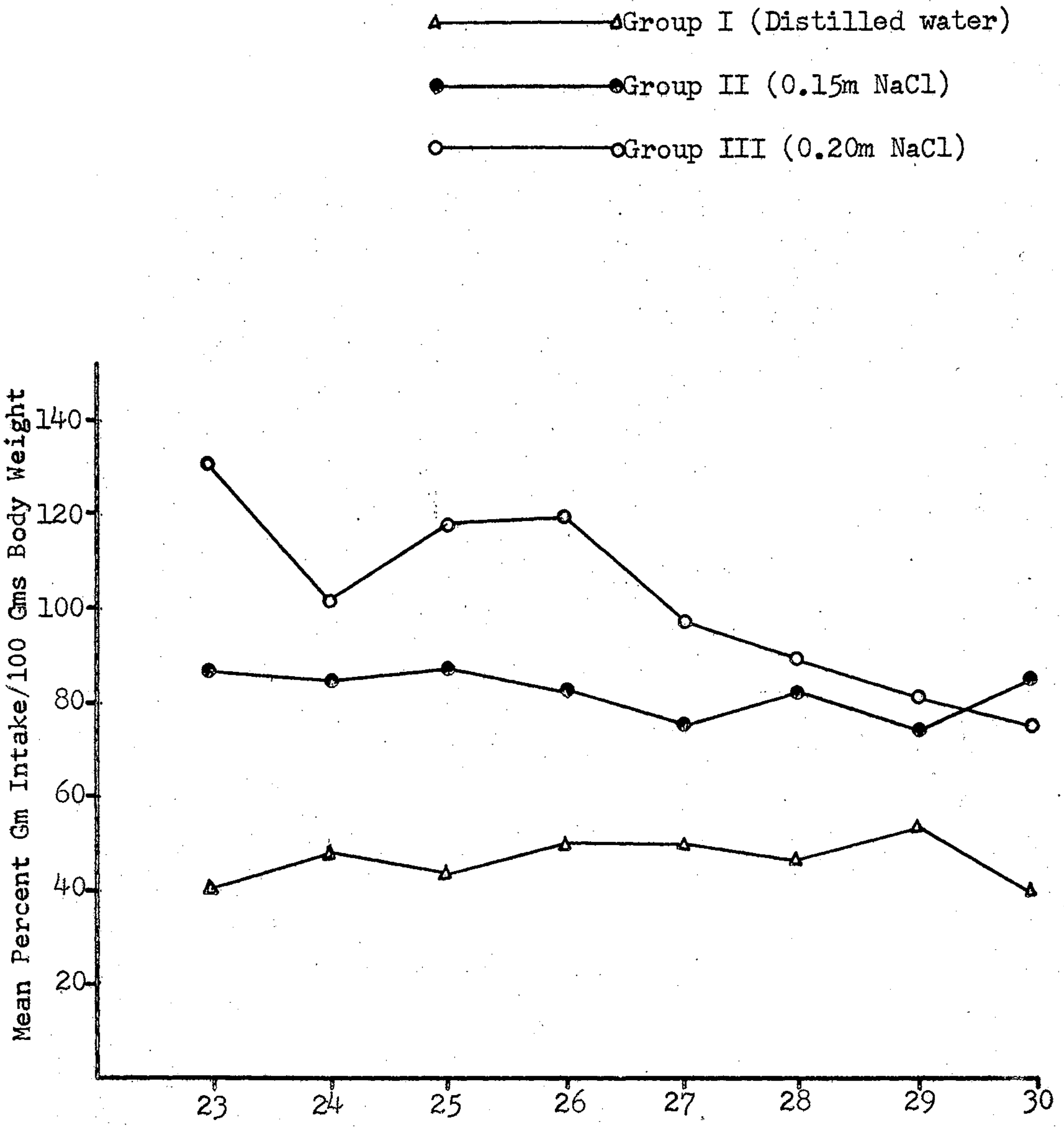

Figure 2. Liquid Intake/100 gms Body Weight for Last Eight Days of Adaptation.

## TABLE II

## SUMMARY OF ANALYSIS OF VARIANCE

| Source | df | MS | F |
|---|---|---|---|
| Between subjects | 11 | | |
| A (adaptation level) | 2 | 25649.56 | 13.40 * |
| Subjects within groups | 9 | 1914.21 | |
| Within subjects | 84 | | |
| B (Blocks of days) | 7 | 578.31 | 4.81 * |
| A x B | 14 | 576.38 | 4.79 * |
| B x Subjects within groups | 63 | 120.21 | |
| Total | 95 | | |

* Significant at the .01 level

significant ($F = 22.79$, $df = 2/9$, $P < .05$). The simple effects of of adaptation level were also significant at Day 30 ($F = 6.25$, $df = 2/9$, $P < .05$).

Using the Newman-Kuels test (Winter, 1962, pp. 298-314), individual comparison of mean percent intake/100 gms body weight/daily 20-hour period at Day 23 showed Group III (129.0) to be significantly greater than Group II (86.7), and Group II significantly greater than Group I (40.4; $q = 4.56$, $df = 1,72$, $P < .005$ and $q = 4.99$, $df = 1,72$, $P < .005$ respectively). Comparisons of mean percent intake/100 gms body weight/daily 20-hour period on Day 30 indicated that Group III (74.6) was not significantly different from Group II (85.4; $q = 1.17$, $df = 1,72$);

however, Group II mean percent intake/100 gms body weight/daily 20-hour period was still significantly greater than Group I (40.1; q = 3.72, df = 1,72, $P < .005$).

The simple effects of Days on Group III were significant ($F = 13.14$, df = 7/63, $P < .01$). As suggested by Figure 2, the simple effects of Days on Group II and Group I were insignificant ($F = .050$, df = 7/63, and $F = .654$, df = 7/63).

## Tolerance

Weights. In Figure 3 body weight during the first 76 hours of the tolerance schedule is plotted as mean percent of the group's initial body weight. The tolerance data were analyzed by a 3 x 7 factorially arranged analysis of variance with repeated measures (Table III).

The effects of adaptation level (A) and time-blocks (B) were significant (Table III). Main effects of adaptation level indicated that Group III (97.1) was significantly greater than Group II (89.7; q = 4.58, df = 1,15, $P < .005$); however, Group II was not significantly different from Group I (87.2; q = 1.15, df = 1,15, $P < .10$). Analysis of the main effects of B showed a significant drop in mean weight for all groups from 4-hours to 76-hours (q = 13.27, df = 7,90, $P < .005$).

Intakes. Amount of the 0.25m NaCl solution consumed by the three groups on the tolerance test is plotted in Figure 4 as the cumulative average group mean percent of 0.25m NaCl consumed/100 gm body weight. Plotted in this fashion, the amount of solution a group consumed relative to its body weight at any point in time can be determined. Also the consumption of a hypertonic saline solution could be expected to exhibit a cumulative effect on the organism as a function of time.

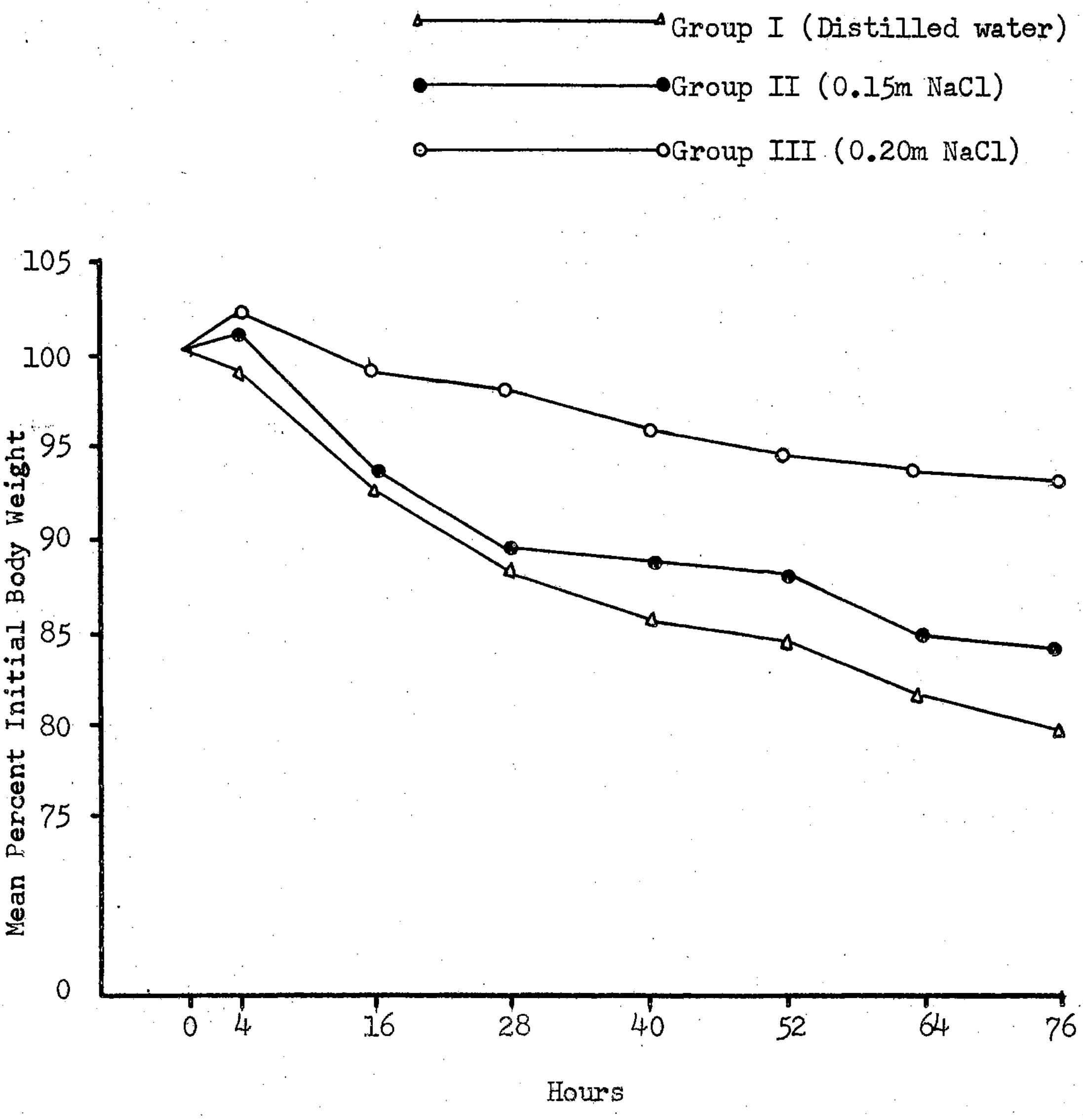

Figure 3. Average Percent Weight Loss During Tolerance Test.

## TABLE III

## SUMMARY OF ANALYSIS OF VARIANCE

| Source | df | MS | F |
|---|---|---|---|
| Between Subjects | 17 | | |
| A (Adaptation level) | 2 | 1101.92 | 13.21* |
| Subjects within groups | 15 | 83.40 | |
| Within Subjects | 108 | | |
| B (hours-time blocks) | 6 | 537.41 | 31.57* |
| A x B | 12 | 29.42 | 1.73 |
| B x subjects within groups | 90 | 17.02 | |
| Total | 125 | | |

*Significant at the .01 level

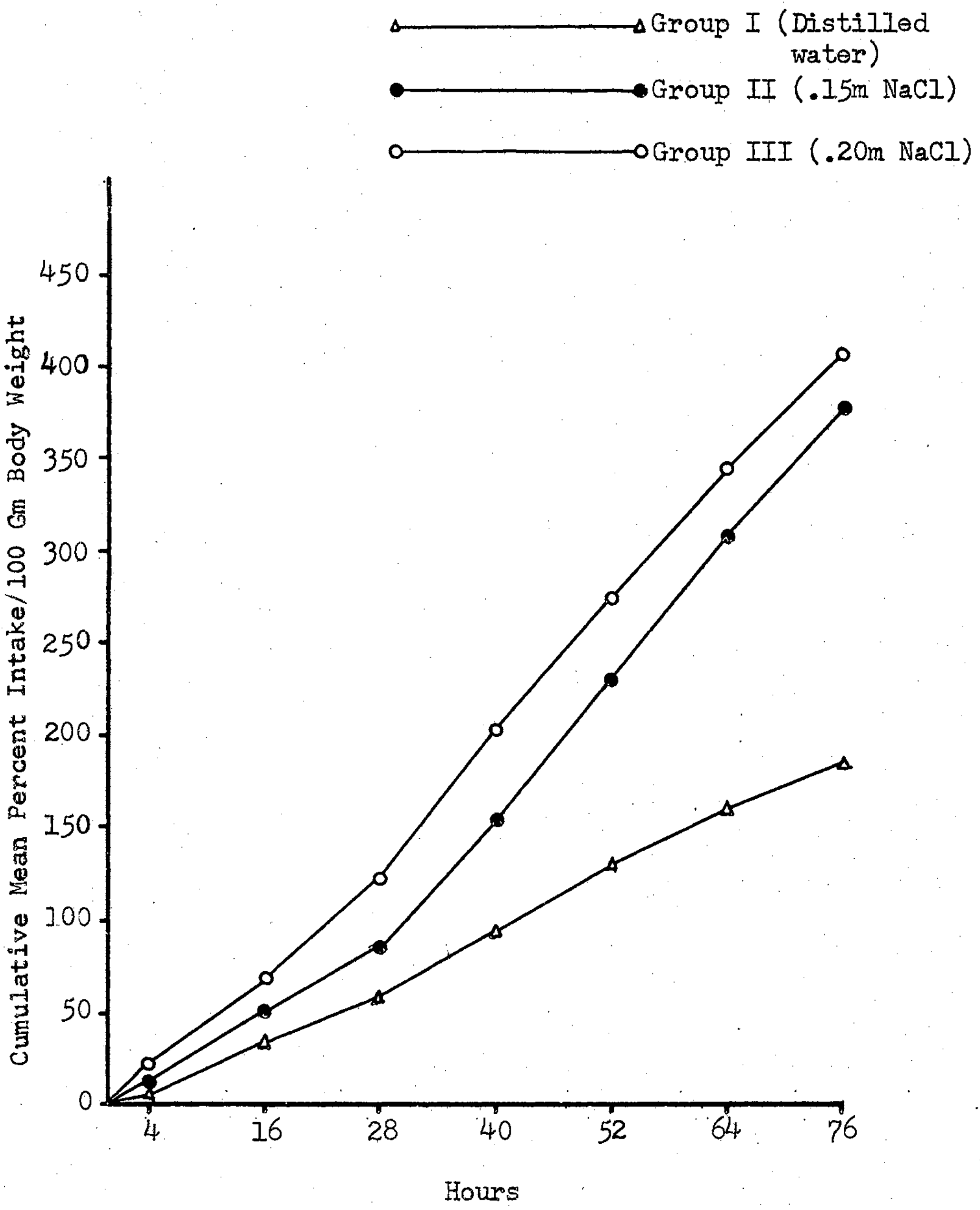

Figure 4. Cumulative Average Group Percent Intake of .25m NaCl Solution/100 gms Body Weight.

Figure 4 shows the average total amount of the hypertonic NaCl solution each group has consumed for each time period. Statistical analysis of the terminal cumulative intakes revealed that Group I (178) consumed significantly less of the hypertonic solution than Group II (376) or Group III (410) ($t = 2.29$, df = 10, $P < .025$, and $t = 3.87$, df = 10, $P < .005$ respectively). Group II and Group III did not significantly differ in terms of terminal cumulative intake ($t = 0.38$, df = 10), although the curves do not overlap and are in the expected direction (Winer, 1962, pp. 24-33).

Survival. The number of Ss in each group surviving each of the 10-24-hour tolerance tests is shown in Table IV.

TABLE IV

DAYS OF SURVIVAL

Days

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
|---|---|---|---|---|---|---|---|---|---|---|
| Group I | 6* | 6 | 6 | 4 | 4 | 4 | 4 | 3 | 3 | 3 |
| Group II | 6 | 6 | 6 | 6 | 5 | 4 | 4 | 4 | 4 | 4 |
| Group III | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 5 | 4 | 4 |

*Number of subjects still alive (six to a group)

## Preference

In the two-bottle drinking tests the percentages of preference (or aversion) were computed by dividing the quantity of the comparison solution ingested by the total quantity of fluid consumed (comparison + standard solution). For example, if a subject consumed the same amount of both solutions, the preference was 50%. Values below 50% suggested aversion. Results of the two-bottle preference test appear in Figure 5. Each point represents the mean of 10 Ss. The data were analyzed by a 3 x 8 factorially arranged analysis of variance with repeated measures (Table V). One S was randomly removed from the group having 11 Ss in order to have an equal number of Ss in each group.

Although the F value was insignificant (Table V) for adaptation level (A), two individual comparison tests appeared appropriate. Of interest was the effect of prior adaptation to a particular NaCl concentration on preference for that same solution when offered a choice between it and distilled water. More specifically, would Group II show a greater preference for 0.15m NaCl and Group III a greater preference for 0.20m NaCl than Group I for the same solutions? Individual comparisons of mean percent preference indicated that Group II (41.9) showed greater preference for the 0.15m NaCl solution than did Group I (34.8) ($q = 1.89$, $df = 1,27$, $P < .05$). Moreover, Group III (39.9) revealed a greater mean percent preference for the 0.20m NaCl solution than Group I (25.4) ($q = 3.91$, $df = 2,27$, $P < .05$).

The main effects of solutions (B) showed the following patterns of significance for adjacent means:

0.10m NaCl 0.15m NaCl: $q = 3.42$, 1,189 $df$. $P < .005$
0.15m NaCl 0.20m NaCl: $q = 2.16$, 1,189 $df$. $P < .025$

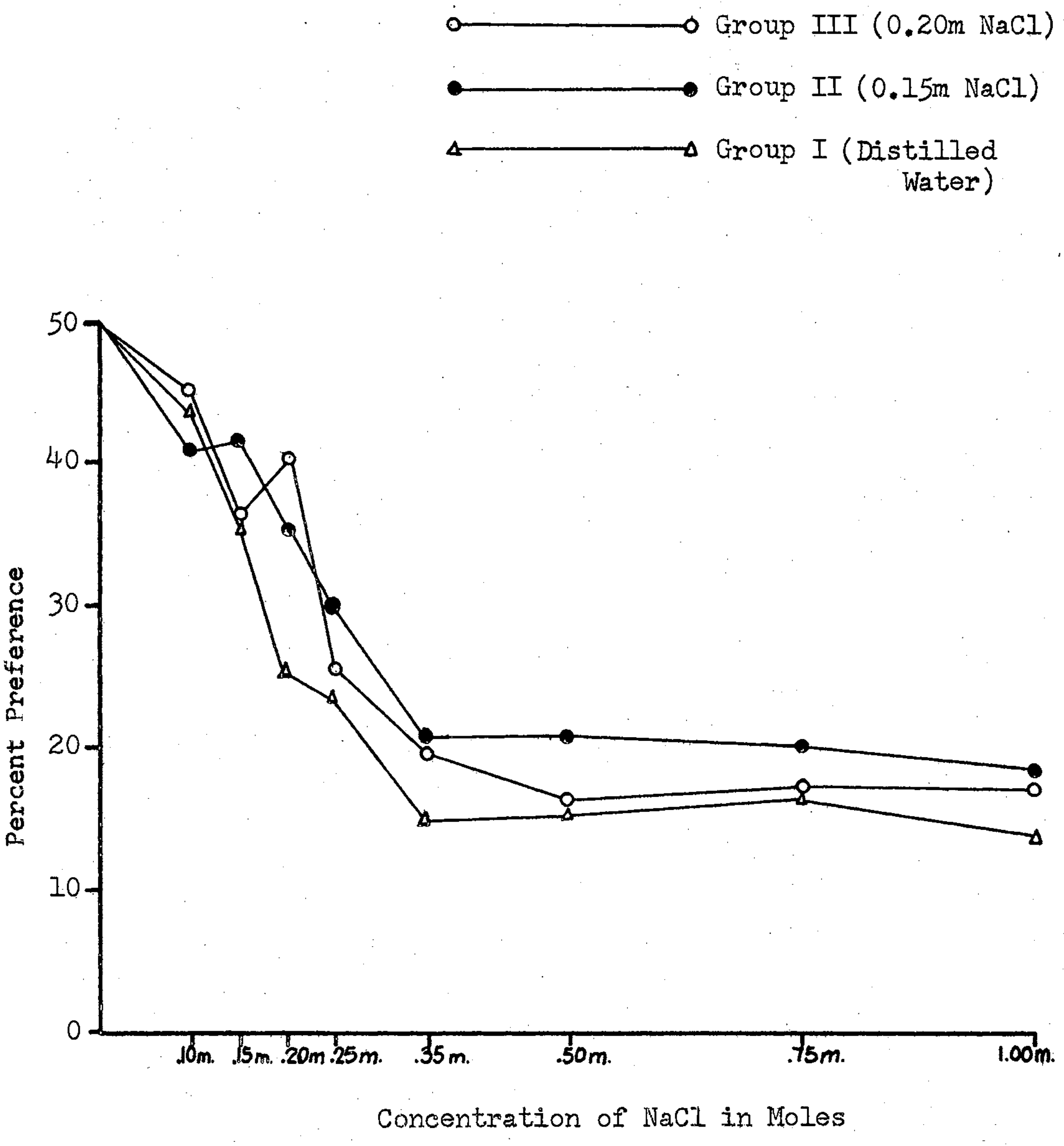

Figure 5. Mean Percent Preference (Aversion) for NaCl Solutions Determined by 48-hour Two-bottle Preference Tests.

## TABLE V

## SUMMARY OF ANALYSIS OF VARIANCE

| Source | df | MS | F |
|---|---|---|---|
| Between subjects | 29 | | |
| A (adaptation) | 2 | 569.90 | 1.20 |
| Subjects within groups | 27 | 476.47 | |
| Within subjects | 210 | | |
| B (solutions) | 7 | 3296.21 | 36.54* |
| A x B | 14 | 88.84 | .98 |
| B x subjects within groups | 189 | 90.20 | |
| Total | 239 | | |

*Significant at the .01 level

0.20m NaCl 0.25m NaCl: *q* = 4.27, 1,189 *df*. *P* < .005
0.25m NaCl 0.35M NaCl: *q* = 4.54, 1,189 *df*. *P* < .005

No significant differences occurred between adjacent means for solutions greater than 0.35m NaCl.

# CHAPTER V

# DISCUSSION

## Adaptation

Figure 2 shows that liquid intake was a positive function of the salinity of the solutions that the subjects were consuming on Day 23. Of the studies reviewed, only certain subspecies of Savannah sparrows (Cade and Bartholomew, 1959) and California quail (Bartholomew and MacMillen, 1961) failed to show increased liquid consumption for rising molarities of NaCl solutions substituted for drinking water.

No physiological measures, such as blood pressure or extent of renal hypertrophy, were taken during the adaptation period, but the group consuming the hypertonic .20m NaCl solution (Group III) was presumably under more stress than was the group consuming the nearly isotonic 0.15m NaCl solution (Group II). Indirect evidence that some physiological changes must have occurred in Group III, in contrast to Group II and Group I, came from tracing the liquid intake as revealed by Figure 2 and statistical tests of simple effects of days. Group III, in contrast to Groups I and II, showed significantly decreased liquid intake across days. In relating these findings to Selye's theory of adaptation, it can be hypothesized that the intake of the distilled water or the 0.15m NaCl solution was not stressful enough to stimulate adaptation in the most efficient organs for dealing with the stress (probably the kidneys in this case). The decline in intake for the group consuming the 0.20m NaCl solution (Group III) may be taken as indirect evidence that the intake of the hypertonic NaCl solution was stressful enough to stimulate some improvement in the group's ability to cope with hypertonic NaCl solutions and that possibly some adaptation occurred in such organs as the kidneys. Generalizing from Figure 2, Group I represented the normal amount of liquid intake since they experienced the least amount of salt stress possible. Group II exhibited accelerated intake and did not alter its consumption across days. This probably resulted from little or no adaptation. Group III, like Group II, increased its liquid intake as an auxiliary mechanism for dealing with the increased salt load; unlike Group II, however, Group III showed decreased consumption across days as a result of improved efficiency in coping with the stress.

## Tolerance

The results of the tolerance test confirmed the above hypothesis that Group III did increase in efficiency in dealing with increased salt loads, although physiological measures were not taken. Presumably, some critical amount of stress or concentration of NaCl is necessary before adaptation will occur. Group II (0.15m NaCl solution) was not statistically different from the nonadapted Group I (distilled water), while Group III (0.20m NaCl solution) was significantly superior to both Group I and Group II in its ability to utilize the hypertonic 0.25m NaCl solution used in the tolerance test. The results of the tolerance test fit well with the hypothesis that the subjects could be adapted to higher levels of stress by having prior experience or prior adaptation to lower levels of stress; however, for adaptation to occur the lower levels of stress must be severe or intense enough to lead to specialization and improvement of function in the most efficient mechanism for dealing with the stress. The extent of resistance to future, higher levels of stress is a function of the amount and extent of prior conditioning that has taken place. It is not possible to glean from the data the length of time over which this increased superiority in coping with the stress is functional, but it is apparent that it was capable of extending the survival of Group III (Table IV). As pointed out by Selye (1956), however, adaptation to high levels of stress tends to be temporary and eventually it results in exhaustion of the organism, as if the reserve adaptation energy has been depleted. The liquid intake of the 0.25m NaCl solution (Figure 4) during the tolerance test indicated that Group III and Group II consumed significantly greater amounts of the hypertonic solution than did Group I.

One hypothesis for predicting preference would be that the prior experience of Groups II and III with saline solutions resulted in less aversion to the 0.25m NaCl solution, whereas the salt-inexperienced Group I showed a greater tendency to reject the solution during the tolerance test. Although the intake of Group II was high and not significantly different from that of Group III, the tolerance test (Figure 3) revealed that apparently only Group III was able to utilize the hypertonic solution in order to maintain body weight.

## Preference

Given the above differences in intake of the tolerance test solution, group differences in salt preference could be expected. There are two opposing sets of results that might be expected from the preference test. First, based on a large amount of conjecture and the studies reviewed that noted a relationship between salt preference (or aversion) and various states of hypertension, an increased salt aversion for Group III, relative to Groups I and II, might be expected. However, no measure of blood pressure was taken and there is no evidence that any of the groups were hypertensive. The second possible prediction would be that since Group III is known to have a higher level of salt tolerance, Group III would show decreased salt aversion relative to Groups I and II. Presumably the salt-tolerant Group III Ss could consume larger quantities and higher concentrations of NaCl solutions relative to Group I and Group II. This should result in less aversion (greater preference) for NaCl for Group III relative to Groups I and II. Because physiological measures such as hypertension and urine chloride were not taken, only indirect evidence of the underlying process is available. However, it has been shown that physiological adaptation, for example, increased renal efficiency, can occur without suffering hypertension (Jelînek and Musilova, 1965).

The statistically insignificant test of the main effects of adaptation level on preference (Table V) indicated that for the eight solutions tested, prior adaptation did not consistently alter salt preferences. Two individual comparisons of means were regarded as appropriate on a post hoc basis. Although the overall responses to NaCl solutions did not vary significantly among groups, it was possible that salt preferences were altered, but only for the particular concentrations the groups were preadapted to drinking. Individual comparisons of mean percent preference indicated that this was the situation. The 0.15m NaCl adapted Group II showed a significantly greater preference for the

0.15m NaCl preference test solution than did the distilled water adapted Group I. Likewise, the 0.20m NaCl-adapted Group III showed a significantly greater preference for the 0.20m NaCl preference test solution than Group I. It can be concluded that salt preferences were not greatly affected by the prior adaptation schedule used in this study. The experience of drinking a specific concentration of NaCl does appear to make the same NaCl concentration less aversive. Binding the kidneys or in some other way specifically inducing a state of hypertension in the bird might possibly reverse the effects and result in greater salt aversion for the hypertensive bird. Further experimentation should reveal whether the slightly altered preferences that occurred in this study were related to changes in salt tolerance or were simply a function of some taste factor determined by prior experience with the NaCl solution.

The final point of interest were the significant differences in preference for different levels of NaCl concentration up to a concentration of 0.35m NaCl; these differences indicated the Japanese quail were capable of discriminating between the various NaCl solutions less than 0.35m NaCl. Several of the solutions discriminated among were below the concentration the birds can maximally tolerate (approximately 2.00m NaCl). In this instance, the behavioral taste preference (aversion) was adaptive. The exact relation between an organism's salt preference and the concentration that it can maximally tolerate has not yet been fully determined.

# CHAPTER VI

## SUMMARY

Fifty-five 20-day-old Japanese quail were divided into three groups. For 30 days each group was adapted to drinking distilled water, 0.15m NaCl or 0.20m NaCl. Following the 30 day adaptation period, 18 Ss were given a salt tolerance test that consisted of a 0.25m NaCl being the only water present for 10 days. Also, the remaining thirty-one Ss were given eight 48-hour two-bottle preference tests in which distilled water was the standard solution and eight molarities of NaCl (0.10m to 1.00m) served as the comparison solutions.

The results suggested that the biological capacity to tolerate a hypertonic saline solution may be a positive function of the concentration of NaCl the Ss are adapted to drinking. The preference test results indicated that the percent preference for the adaptation concentrations of NaCl (0.15m and 0.20m) was significantly altered and found to be less aversive for the two salt-experienced groups of Ss relative to the single salt-inexperienced group. Increased renal efficiency was suggested as the mechanism used for increased biological capacity in the tolerance test; whereas, preference test behavior appeared to be more closely related to the particular NaCl concentration experienced during adaptation by the Ss. The results were discussed as being in accordance with Selye's theory of adaptation to stress.

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