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THE DEVELOPMENT OF THERMOREGULATION IN THE BOBWHITE QUAIL

By

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ABSTRACT

THE DEVELOPMENT OF THERMOREGULATION IN THE BOBWHITE QUAIL

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Adult and immature (1 to 65 day old), unanesthetized bobwhites (Colinus virginianus) were exposed to a wide range of ambient temperatures (T_a) in a chamber in which T_a, relative humidity and air flow were controlled. Evaporative heat loss (E), metabolic heat production (M) and internal body temperature (T_b) were determined for steady-state exposures. Growth and thermoregulatory development of the bobwhite was divided into 3 stages. These stages included day 1 to day 6 (Stage I), day 6 to day 14 (Stage II) and day 14 to the adult (Stage III).

In Stage I, there was limited increase in body mass or plumage growth. The bobwhite was unable to maintain a stable T_b above T_a when exposed to T_a 20C. Internal body temperature increased 3C at T_a 25 and 30C due to an increase in M from day 1 (1.5 watt/g x 10^{-2}) to day 6 (2.4 watt/g x 10^{-2}). Dry thermal conductance increased from .20 watt/g/C x 10^{-2} to .36 watt/g/C x 10^{-2} at both T_a 35 and 25C. Percentage of total heat loss by evaporation did not change significantly during Stage I, indicating that E did not

contribute to the inability of the 1 to 6 day old quail to maintain an adult T_b. The major contributor to the increase in T_b during Stage I was the increase in M.

In Stage II, T_b approached adult T_b (41C) at T_a 30 and 35C, but was significantly lower (37C) than adult T_b at T_a 25C. Metabolic heat production did not increase during Stage II. Thermal conductance decreased from .54 watt/g/C x 10^{-2} to .28 watt/g/C x 10^{-2} between 6 and 14 days after hatching. Evaporative heat loss did not change significantly during Stage II. Increase in thermal insulation was the major contributor to the increase in T_b during Stage II.

In Stage III, body growth rate increased from 1.7 g/day before day 20 to 2.8 g/day afterwards. The major decrease in estimated surface area to mass ratio occurred by 20 days after hatching. By 25 days after hatching, the quail was capable of increasing M at T_a 15C above the 30C level. After day 25, there was a parallel, age-dependant decrease in M versus T_a due to an increase in thermal insulation. Evaporative heat loss did not change significantly after 18 days. The major changes which characterized Stage III included an increase in M at T_a 20C and continued increase in thermal insulation as a function of age.

Plasma triiodothyronine (T_3) and thyroxine (T_4) levels were elevated at hatching and decreased from day 1 to day 10 after hatching. No significant change in plasma T_4 levels occurred after day 10. Plasma T_3 levels increased

significantly from day 21 to day 29 after hatching and remained above the adult level (300ng%) through 65 days. Half-life of plasma T_3 was significantly lower at 21 and 45 days (3.2hr) than in the adult (5hr), indicating that more T_3 was produced between 21 and 45 days after hatching than in the adult. Such an increase in T_3 could possibly contribute to the ability of the 25 day old to maintain a stable M at T_a 20C.

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INTRODUCTION

It is well recognized that a newly hatched bird is unable to maintain a stable internal body temperature when exposed to a range of ambient temperatures. This lack of homeothermic ability is attributed to numerous factors including the young animal's large surface area-to-volume ratio, its inability to maintain a high metabolic heat production for an extended period of time, its insufficient thermal insulation (due to reduced vasomotor control and a lack of plumage quantity and quality) and its large evaporative heat loss. Although the adult bird is a stable homeotherm, there is little knowledge concerning the ontogenetic development of these thermoregulatory parameters.

Studies of homeothermic development can be conducted with greater precision for the bird than they can be for mammals, since much of mammalian physiological and anatomical maturation occurs in utero, whereas the bird is available in an early developmental stage at the time of its hatching. Further, environmental factors affecting thermal responses are more easily controlled for the young bird than they are for the mammalian neonate.

Although there have been many earlier studies of the

development of body temperature control in birds, many of these have examined only a few ages of the animal and have sampled only sparcely within a range of ambient temperature. Few studies have evaluated separately the animal's transient and steady-state adjustments to controlled thermal stress, and few have measured simultaneously an adequate number of physiological responses to this stress.

I have chosen to study the thermoregulatory development of the bobwhite (Colinus virginianus). This species is native to a large area of the United States and is found as far north as Michigan and as far south as Florida. This geographical distribution implies that the bobwhite is able to survive a wide range of thermal exposures during its maturation. In addition, this species is a popular game bird and constitutes a major environmental resource. Also, there is little quantitative information about the development of thermoregulation for this species.

The present study was designed to examine the normal development of homeothermy in the bobwhite from hatchling to adult form. Experiments were conducted on animals of many different ages in controlled tests ranging from hypothermic to hyperthermic thermal stress. In addition to measurements of body temperature, metabolic heat production, evaporative heat loss and other determinants which define the physiological responses of the unanesthetized, unrestrained animal to controlled thermal stress, thyroid hormone metabolism and plasma levels were measured and evaluated in

respect to the animal's thermoregulatory ability. These data provide new information about the development of thermoregulation in the bobwhite and define more completely the thermoregulatory competency of this species.

The maintenance of a relatively constant body temperature requires a balance of heat inflow, production and outflow, as stated in the body heat balance equation (Bligh and Johnson, 1973) which indicates that the rate of storage of body heat (S) is equal to the metabolic heat production (M) plus or minus the energy exchanged by evaporative heat transfer (E), radiant heat transfer (R), convective heat transfer (C), conductive heat transfer (K), and work (W). That is:

$$S = M \pm E \pm R \pm C \pm K \pm W \qquad (1)$$

Many mammals at birth have a relatively mature thermoregulatory system (lambs-Alexander and Williams, 1968; guinea pigs-Blatteis, 1975; humans-Bruck, 1978). This implies that a large portion of mammalian thermoregulatory development occurs during embryonic and fetal growth in the thermally stable environment of the uterus. In contrast, birds may be exposed to a wide range of environmental conditions during embryonic development and vary markedly among species in their thermoregulatory ability at the time of hatching.

Hatchlings are classified as altricial, precocial, or intermediate. Altricial hatchlings possess little or no plumage, lack muscle development and rely heavily on adults for both food and warmth. They include birds in the orders Columbiformes and Passeriformes (Dawson and Hudson, 1970).

Most precocial hatchlings are covered with down, are able to move about, feed themselves and display a more mature thermoregulatory ability than the altricial young. Precocial hatchlings are those in the orders Anseriformes, Charadriiformes, and Galliformes (Dawson and Hudson, 1970). Other hatchlings, such as common nighthawks and shearwaters, display an intermediate thermoregulatory ability (Dawson and Hudson, 1970). Development of adult thermoregulatory ability occurs at a faster rate in precocial than in altricial species (Whittow, 1976a).

The attainment of homeothermy in birds requires the coordinated development of many related functions, including changes in thermal insulation, evaporative water loss, body weight, surface area-to-volume ratio, behavior, food consumption, basal metabolism, shivering and nonshivering thermogenesis, and thyroid hormone metabolism. The ability to control heat production and heat loss is also necessary. Specific mechanisms used by most adult birds for thermoregulation have been extensively reviewed (Dawson and Hudson, 1970; Freeman, 1971b; Calder and King, 1974; Whittow, 1976a). This review will be limited to avian thermoregulatory development. Adult thermoregulation will be presented only in the context of its relationship to the ontogenetic process.

II. Body Temperature

The internal body temperature of adult birds is usually higher than that for adult mammals of comparable size, although there is some overlap (Prosser, 1973; Whittow, 1976a). McNab (1966) suggested that birds are able to maintain a body temperature several degrees higher than mammals because they have a higher weight-specific metabolic rate and a lower heat loss rate. Most adult birds are able to maintain a body temperature of approximately 40C. Calder and King (1974) proposed that the elevated body temperature enables the bird to save water and prevent desication, but not necessarily save energy. By maintaining a high body temperature, there is less requirement for evaporative cooling and, consequently, a greater reliance on conductive, convective and radiative mechanisms for heat dissipation.

The difference between avian and mammalian body temperatures is nearly matched by inter- and intraspecies differences among avian species. The bodies of small birds and mammals have higher heat transfer coefficients than those of larger animals (Herried and Kessel, 1967) due to larger surface area-to-volume ratios and less thermal insulation per unit surface area. Despite the high heat transfer rates of small birds, they generally have a higher body temperature than do large birds (38.1C body temperature for the emu; Crawford and Lasiewski, 1968, 41.3C for the California quail; Brush, 1965). McNab (1966) showed that some small birds have a higher weight specific metabolic

rate than do larger birds, and suggested that this produces the elevated body temperature. There are, however, exceptions as demonstrated by the adult hummingbird which may have a body temperature as low as 35.6C. Borchelt and Ringer (1973) demonstrated that the body temperatures of young bobwhite increased with repeated handling. This type of disturbance might be one reason for the large differences in body temperature seen by various investigators. The many exceptions to the "inverse body size-temperature" relationship lead Calder and King (1974) to state that bird body temperatures measured under resting conditions are not related to body size. It is unclear whether large interspecies differences actually exist or are due to sampling errors.

Differences in body temperature among bird species are linked to the interrelated influences of animal size, activity, photoperiod, environmental temperature, season, and endogenous factors. Birds have diurnal fluctuations in body temperature in most environments, with the highest temperature reached during the day and the lowest reached at night (Simpson and Gilbraith, 1905; Irving, 1955; Bartholomew and Dawson, 1958; Heath, 1962; Howell and Bartholomew, 1962; MacMillen and Trost, 1967). A large part of this diurnal variation is due to daily changes in activity and metabolism (Hudson and Kimzey, 1966; Dawson, 1958; Pohl, 1969), with the increase in activity followed by an increase in metabolism and body temperature. The low

metabolic heat production and body temperature at night may be an energy saving mechanism used during cold exposure (Steen, 1958; MacMillen and Trost, 1967) and/or when food supply is limited (Warham, 1971) to reduce the need for mobilization of internal food stores.

Endogenous factors may influence body temperatures of birds (Hudson and Kimzey, 1966; MacMillen and Trost, 1967; Coulombe, 1970), in view of the rise in body temperature of some birds several hours before the daily light cycle. Washburn (1962) noted that the amplitude of the temperature fluctuation in chickens was reduced by feeding thiouracil. This suggests a relationship between thyroid activity and body temperature. Numerous internal factors could influence internal body temperature, but they have received only limited investigation.

Adult birds, when exposed to ambient temperature extremes, may display different forms of adaptation. Scholander et al. (1950a) showed no difference in body temperatures of birds and mammals adapted to different climates, and this suggested that the primary thermoregulatory difference among them was due to their thermal insulation and their control of heat loss (Scholander et al., 1950c). Steen (1957) noted that adult pigeons acclimated to ambient temperatures of -10C, +18C, and -24C for 2-4 weeks displayed a diurnal fluctuation in cloacal temperature of 1C, but showed no difference in cloacal temperatue as a function of ambient temperature.

However, birds raised at high environmental temperatures increase body temperature several degrees above the normal body temperature (Bartholomew and Dawson, 1958; Brush, 1965; Murrish, 1970; Coulombe, 1970). The tolerance of an elevated body temperature allows the birds to maintain a positive heat loss when the ambient temperature equals the bird's thermoneutral body temperature.

The range of body temperature among birds is inversely related to body size. The hummingbird and swift have a 9C range (Neumann, et al., 1968) and the ostrich maintains a fairly constant body temperature throughout the day (Crawford and Schmidt-Nielsen, 1967). This variance in body temperature is related to surface area-to-volume ratio and insulation differences among birds of different size. Heat transfer in small birds is faster than in large birds for the same thermal stress which could increase the daily rate of heat exchange and produce larger fluctuations in body temperature.

Signs of thermoregulation appear in most birds during embryonic development. There have been few investigations into the changes in thermoregulatory ability of the embryo because of difficulties in measuring low levels of metabolism and the assumption that there is little, if any, development of thermoregulation during this time. Evidence suggests that it is impossible for the chick embryo to regulate successfully its body temperature during early development (Romijn, 1954; Romijn and Lokhorst, 1955).

During the first 10 days of incubation, evaporative heat loss is greater than heat gain and there is no change in egg temperature. Heat production exceeds heat loss after day 10, when embryo temperature increases from 37.9 C to approximately 39.0 C at hatching. Romanoff (1941) noticed that chicken embryo temperatures increased approximately 3 C over the 19 day incubation period. Japanese quail embryos show no increase in their resistance to cooling at 30 C before 9 days of incubation (McNabb et al., 1972). Although there is some endothermic ability in the Japanese quail before hatching, it does not establish a homeothermic state, nor is it achieved in other species (western gull-Bartholomew and Dawson, 1952; mallards, scaups-Untergasser and Hayward, 1972). McNabb et al. (1972) suggested that any increase in resistance to cooling before hatching is likely due to embryo muscle activity rather than a decrease in its thermal conductance.

There are large variations among species in the thermoregulatory ability of hatchlings and the time required for the development of homeothermy. Mallard ducklings probably acquire homeothermy faster than do any other avian forms, and are able to maintain a near constant body temperature when exposed to 1-2C ambient temperature one day after hatching (Untergasser and Hayward, 1972; Caldwell, 1973). Thermoregulation develops in mallards in two phases. The first begins 1-2 hours after hatching and is due to an increase in thermal insulation as the down dries. The

second occurs 16-24 hours after hatching in response to physiological changes (i.e. increase in metabolism, growth). Other birds, such as the herring gull (Dunn, 1976), scaups and common eiders (Untergasser and Hayward, 1972), are able to maintain a constant body temperature when exposed to extreme environmental temperatures only a few days after hatching. Others increase body temperature over a more prolonged period. Core and surface temperatures of the domestic chicken rise over the first 22 days after hatching (Randall, 1943; Allen and Marley, 1967) with the largest increase occuring in the initial 4 days (Lamoureux and Hutt, 1939; King, 1956).

Some birds undergo a large portion of their thermoregulatory development during the first week after hatching. These include the Lapland longspur snow bunting (Maher, 1964), field and chipping sparrows (Dawson and Evans, 1957) and willow ptarmigans (Aulie, 1976a). The majority of the birds, however, develop homeothermic regulation and maintenance of adult body temperature during the first two weeks after hatching (ring-necked pheasants-Morton and Carey, 1971, Ryser and Morrison, 1954; willow grouse-Myhre et al., 1975; house sparrows-Blem, 1975, Seel, 1969; house wren-Odum, 1942, Kendeigh, 1939; cactus wrens-Ricklefs and Hainsworth, 1968; Japanese quail-Spiers et al., 1974; emperior and adelie penguins-Goldsmith and Sladen, 1961; doublecrested cormorants-Dunn, 1976; cattle egrets-Hudson et al., 1974). A few species of quail do not

reach adult body temperature until 4 weeks after hatching (bobwhite-Borchelt and Ringer, 1973; Chinese painted quail-Bernstein, 1973).

During the first few days after hatching, the body temperature of the bird may vary several degrees daily (Kendeigh and Baldwin, 1928). This is attributed to photoperiod (Bartholomew, 1953; Goldsmith and Sladen, 1961) with the mean, night body temperature being several degrees lower than the day body temperature. The body temperatures of hatchlings may also vary as a function of ambient temperature (Dawson et al., 1972; Aulie, 1976a; Dawson et al., 1976). Body temperatures of hatchlings vary over a wider range than do adult body temperatures. The maintenance of a high body temperature during exposure to elevated ambient temperatures allows the bird to continue using dry thermal conductance pathways and depend less on heat loss by evaporation. Low body temperatures during cold exposure reduces the requirement for high metabolic heat production and allows the animal to survive with limited thermal insulation and food intake.

The body temperature of young birds may not increase with age until the adult level is reached, but may decrease at some point during the first weeks after hatching (Freeman, 1965; Borchelt and Ringer, 1973). The increase in body temperature and thermoregulatory ability may also be influenced by environmental temperatures. Maher (1964) showed that thermoregulation develops faster at high

environmental temperatures than it does at low temperatures. Others find that birds raised at 35C (McNabb and McNabb, 1977a) or intermittently exposed to cold temperatures (Myhre, 1978) have a higher body temperature than do those raised at a higher ambient temperature. McNabb and McNabb (1977a) suggested that exposure to low ambient temperatures during growth may be a requirement for "normal" thermoregulatory development.

III. Heat Production

A primary requirement for homeothermy is the ability to generate or absorb heat at the same rate that it is lost from the body. Heat must be generated at a faster rate below the animal's lower critical temperature in order to maintain a constant body temperature and compensate for the increased heat flow rate to its environment.

Heat production does not increase in the chick embryo when it is exposed to low ambient temperatures. Kendeigh (1940) noted that the house wren decreased oxygen consumption with a drop in ambient temperature, suggesting a similiar decline in metabolic rate and heat production. Pembrey (1895) found a similiar response in the chick embryo up to day 15 of incubation. Other investigators have found low levels of thermogenesis before hatching. Romanoff (1941) noted that the oxygen consumption of the chick embryo increased sigmoidally up to day 17 of incubation, after which the increase slowed to nearly a steady state level.

McNabb et al. (1972) found that body cooling rates in the Japanese quail embryos do not show a significant decrease until 9-14 days of incubation. He suggested that the decrease in cooling was the result of increased thermogenesis, due to increased embryonic muscle activity. The willow ptarmigan also shows no sign of thermoregulation until after 2 weeks of incubation (Aulie and Moen, 1975). The fully developed chick embryo when exposed to a low ambient temperature experiences only a 26% decrease in metabolic rate. The embryo is not able to maintain heat balance at this time, and shows only a passive response to changes in ambient temperature (Pembrey, 1895).

Only when the bird begins to hatch is there a large increase in metabolic heat production. The willow ptarmigan increases its CO_2 production 3-fold (.39 ml/g/hr to 1.13 ml/g/hr) while emerging from the shell (Aulie and Moen, 1975). Oxygen consumption increases in the chick embryo approximately 3-4 hours before hatching. Freeman (1962) suggested that the stimulus for increasing metabolic rate is when the beak enters the egg air sac and pulmonary respiration begins. When breathing begins, the bird uses more energy for respiration and thereby has a higher metabolic rate. This increase is accompanied by a transient homeothermic response to cold temperatures which may occur as early as 19 days of incubation (Freeman, 1962).

The body temperature of the domestic chick increases over the first six days after hatching (Freeman, 1965).

Untergasser and Hayward (1972) noted that there was a continuous increase in the metabolic rate of the mallard, scaup and common eider to a peak level 3 days after hatching. During this time, there is little change in the surface area-to-volume ratio of the bird, eliminating it as a possible explanation for the increase in body temperature. Freeman (1965) found that as the yolk sac is depleted it is replaced by more actively metabolizing tissue. The increase in this tissue mass over the first six days after hatching could be the reason for the increase in body temperature.

The weight-specific metabolic rates of Japanese quail (Blem, 1978) and pigeons (Riddle et al., 1932) reach a peak one to two weeks after hatching, after which it declines to the adult metabolic rate level. The metabolic rate of other species also intensifies over the first week after hatching (field and chipping sparrows-Dawson and Evans, 1957; vesper sparrows-Dawson and Evans, 1960; house sparrows-Blem,1975) to two weeks (cattle egrets-Hudson et al., 1974; house wren-Kendeigh, 1939).

The increase in weight-specific metabolic heat production after hatching is associated with a period of rapid growth and homeothermic development. Barott and Pringle (1946) and Freeman (1967) found that with the increase in metabolism there is a decline in the lower critical temperature and a widening of the thermoneutral zone. A similiar response is found in the Japanese quail hatchling, with the 1 week-old displaying a thermoneutral

temperature of 35C. After one week, this widens into a thermoneutral zone which has a lower critical temperature of 31C (Freeman, 1967).

The metabolic ability of young birds may be altered if they are exposed to cold temperatures during their developmental period. Aulie (1977) found that bantam chicks, after one week of intermittent cold exposure, had a higher maximum metabolic rate than controls. There was no difference in the resting metabolic levels between the two groups, suggesting that the change was in the heat producing capacity of the tissue for oxidative metabolism, rather than an increase in total tissue mass. Hart (1962) noted a similiar increase in the metabolic capacity of adult house sparrows and evening grosbeaks when they were acclimated to winter temperatures. He determined that the increased thermogenic capacity was not due to an increase in nonshivering thermogenesis.

IV. Energy Metabolism

The energy found in birds is often divided into metabolized energy, existence energy, and excretory energy. Metabolized and existence energies are of primary importance in thermoregulatory adjustments. The metabolized energy is the total amount retained in the body. The existence energy is that required for basal metabolism, thermoregulation and specific dynamic activity.

Energy reserves in birds vary as functions of ambient

temperature and age. In adult birds, metabolized energy increases with a decrease in ambient temperature, but the efficiency of food utilization decreases (zebra finch-El-Wailly, 1966; Alaskan redpolls-Brooks, 1968; starlings, crested myna-Johnson and Cowan, 1975). There is an inverse relationship between existence energy and ambient temperature (house sparrows-Kendeigh and Blem, 1974; zebra finch-El-Wailly, 1966; Alaskan redpoll-Brooks, 1968).

Nearly 87% of the adult bird's energy comes from carbohydrate metabolism (Freeman, 1971a), however, fat is the primary energy storage form for the adult, with only partial use of glycogen stores in liver and muscle (Whittow, 1976b). During winter acclimation, house sparrows increase fat storage and the production of unsaturated fatty acids (Barnett, 1970). The titmouse shows no change in total lipid content between summer and winter months (Hissa and Palokangas, 1970).

In the embryo, the primary energy source and the chief storage reserve is fat which is derived mainly from the egg yolk (Freeman, 1971a). The embryo, however, exhibits changes in carbohydrate reserves with a change in ambient temperature. The 14 day-old chick embryo experiences a decrease in liver glycogen with an increase in ambient temperature (Clawson, 1975). There is also a decrease in liver glycogen and blood glucose in the 19 day-old chick embryo when it is exposed to 20C (Freeman, 1967). This suggests that carbohydrate reserves are used during

temperature stress in addition to lipid energy sources. If the 19 day-old chick embryo is further chilled by exposure to 4C, there is no change in glycogen content or blood sugar levels (Freeman, 1966), probably due to a reduction in enzyme function required for glycogenolysis at extremely low temperatures.

Yolk continues to be the primary energy source for young birds until several days after hatching (Riddle et al., 1932; Blem, 1975) while there is a decrease in the caloric content per gram of fresh tissue (Blem, 1975). Several days after hatching, the caloric content per gram of fresh tissue of some birds increases as a result of the increase in lipid content and decrease in water content (Ricklefs, 1967; Blem, 1975; Dunn, 1975). Japanese quail show an increase in body caloric content from 1 kcal/day on day 1 to 8 kcal/day at 22 days of age (Blem, 1978). After this time, the caloric content does not increase as rapidly.

There are also shifts in liver glycogen levels shortly after hatching in the Japanese quail (Okon, 1978). A sharp decrease in liver glycogen occurs at hatching (7.8 mg/g body weight one day before hatching to 1.8 mg/g body weight one day after hatching). The large decrease is probably due to the increased mobilization of energy reserves to satisfy the rise in energy metabolism during hatching (Okon, 1978). A transient rise in liver glycogen occurs on day 5 due to the change from a high lipid to a high carbohydrate diet and to the sudden increase in blood glucose. A second rise occurs

at 2 weeks after hatching which peaks at 3-4 weeks. Okon (1978) suggested that as the bird acquires homeothermic ability (possibly decreasing thermal conductance) there is less weight-specific energy requirement for heat production. If there is little reduction in the rate of food consumption over this period, then the bird would probably place the excess food in liver glycogen stores.

Existence energy, metabolized energy and gross energy intake begin to increase in the house sparrow soon after hatching and reaches a maximum level at 13 days before declining to the adult level (Blem, 1975). Several bird species also show an increase in the efficiency off energy utilization from a low level at day 1 to a high point approximately two weeks after hatching (Japanese quail-Blem, 1978; house sparrow-Blem, 1975). The responses of the 1 day-old chick to cold stress is similiar to that of the embryo. Exposure to cold causes a fall in liver and muscle glycogen stores (Freeman, 1966; Palokangas et al., 1973), increases blood sugar (Palokangas et al., 1973), and a mobilization of lipid stores, as evidenced by a rise in plasma free fatty acid levels (Freeman, 1967). These are similiar to those of the 3 week-old fowl which displays a transient, increased mobilization of carbohydrate and lipid stores and a rise in plasma free fatty acid levels (Freeman, 1976).

V. Growth Rate

The growth rate for many birds is rapid in the first few days after hatching (barnswallows, red-winged blackbirds - Ricklefs, 1967; mountain white-crowned sparrows - Morton and Carey, 1971; vesper sparrows - Dawson and Evans, 1960) and the growth of locomotory organs and integument occurs at a faster rate than that of food processing organs (Ricklefs, 1967). In chicks, the body weight does not increase immediately, but instead drops 10% over the first 2 days after hatching. This is because the chick is metabolizing yolk from the absorbed yolk sac as its only food source and it is not ingesting food. After day 2, body weight increases rapidly until the bird is 3 weeks-old (Wekstein and Zolman, 1971).

In general, there is a parallel relationship between growth rate in young birds and the rate of thermoregulatory development partially because the increased growth rate usually occurs when the animal's metabolic rate is the highest (Whittow, 1976b), although this is not always the case (Riddle et al., 1932). An increased metabolic rate and low thermal conductance are required for the maintenance of an adult body temperature, according to McNab (1970). In birds, metabolic rate closely follows the development of musculature (Dawson and Evans, 1960). Thermal conductance decreases with the reduction in surface area-to-volume ratio and increase in insulation (Dawson and Evans, 1960; Ricklefs and Hainsworth, 1968; Breitenbach and Baskett, 1967; Hudson

et al., 1974; Dawson et al., 1976). Others have shown that increased resistance to cold and the maintenance of an adult body temperature occurs in some birds long before growth is complete or adult insulation has appeared (Gardener, 1930; Freeman, 1965; Wekstein and Zolman, 1971; Dunn, 1976), indicating that growth and animal size are not the only important factors for homeothermy.

The daily food consumption of young birds and their growth rates are temperature dependent (Kleiber and Dougherty, 1934; Barott and Pringle, 1947, 1949, 1950; Kontogiannis, 1968; Vo et al., 1978). The gross energy intake in young (Vo et al., 1978) and adults (Kendeigh, 1949; Steen, 1957; Kontogiannis, 1968) increases with a drop in ambient temperature. There is less efficient digestion and food conversion at low ambient temperatures resulting in an increased excretory energy loss and a decreased growth rate (Kleiber and Dougherty, 1934; Kendeigh, 1949; Osbaldiston and Sainsbury, 1963; Kontogiannis, 1968). Wilson et al. (1957) suggested another reason for the decreased growth at low temperatures was that more energy was being used for body temperature maintenance and less was available for growth and synthesis of protein. This indicates a relationship between growth and thermoregulatory development.

VI. Insulation

Heat flow from the bird occurs by both conduction and convection. Thermal resistance to this flow is partly in the tissue and partly across the plumage.

The rate of conductive heat exchange in body tissue varies as a function of body area, temperature gradient, the intrinsic thermal conductance of the tissue, its effective thermal conductance coefficient, as well as internal and external heat transfer coefficients at the exchanging surfaces. Since cutaneous blood flow to the feathered body areas in the bird is less than it is to the extremities (Wolfenson et al., 1978), conductive heat exchange across the feathered area is low compared to the legs. Heat transfer by conduction across the plumage varies widely because pilomotor reflexes rearrange feather position and alter their thermal conductance. This is an important survival mechanism for birds exposed to either heat or cold stresses.

Convective heat transfer is a principle avenue by which heat moves through an animal's body. It involves the movement of a fluid and the transfer of its heat to the surface of a solid. The influential factors in convective heat flow include the following (Gates, 1962).

1. Fluid velocity
2. Contact surface area
3. Surface properties
   a. Shape
   b. Orientation
4. Fluid properties
   a. Density
   b. Viscosity

c. Specific heat
d. Thermal conductivity
5. Evaporation or condensation
6. Object dimension
7. Boundary layer thickness surrounding object

In animals, blood flow is an important mechanism for forced convective heat transfer within the body. Scholander et al. (1950b) first noted that arctic gulls standing on ice maintained leg and foot temperature just above freezing and body temperature at normal levels. He attributed the high core-foot thermal gradient to vasomotor control in the leg. Later, Baudinette et al. (1976) showed that herring gulls vary blood flow to their feet and have reduced heat loss from the feet with a decline in ambient temperature. Spellerberg (1969) found that the adult McCormick skua decreased web temperature as ambient temperature decreased, while rectal temperature remained stable. Snapp et al. (1977) demonstrated that vasomotion in the California quail was responsive to both hypothalamic and ambient temperatures, with an increase in vasoconstriction occuring at lower ambient temperatures.

The extremities of the bird may also be used for heat transfer during exposure to warm temperatures. Vasodilation of comb and toe blood vessels occur during infrared irradiation before there is an increase in core body temperature (Richards, 1970). Murrish (1970) showed that blood vessels in the legs of the Dipper would alternately constrict and dilate at the animal's upper critical temperature to aid in heat loss.

The ability of birds to maintain extremitity temperature lower than core temperature is not only due to vasomotor activity, but also to an arteriovenous heat exchanger located in the skin and legs. Irving and Krog (1955) described these skin arteriovenous heat exchangers and suggested a mechanism for maintaining foot temperature approximately 40C below body temperature. A complex rete mirabile structure was discovered by Kahl (1963) in the legs of the woodstork that could serve as a possible counter-current heat exchanger to maintain a large core-foot temperature gradient. Steen and Steen (1965) found that the heat exchangers in the legs of birds were extremely effective in controlling heat loss from the animal. They noted that the gull lost less than 10% of its heat across the legs at -16C, whereas at 35C all of the heat generated by the animal was lost by the legs.

In addition to the peripheral vascular adjustments at different ambient temperatures, there are also central cardiovascular changes which aid in heat transfer. Murrish (1970) found that the Dipper increased its heart rate at ambient temperatures above its upper critical temperature, which with alternating constriction and dilation of the peripheral blood vessels increased heat loss. The heart rate of the bird may also increase at ambient temperatures below its thermoneutral zone (Bartholomew et al., 1962; Coulombe, 1970) and aid in supplying oxygen and nutrients to the actively metabolizing tissue, as well as removing carbon

dioxide from the area.

Most evidence suggests that convective heat transfer by blood flow is an extremely effective means of distributing heat throughout the body. Changes in convective heat transfer through vasomotion, many times occur rapidly with changes in ambient temperature and provide an immediate thermal defense.

Scholander et al. (1950a) demonstrated that animals adjust to extreme environmental temperatures not by metabolic changes but by altering skin, fur and plumage insulation. Several investigators have noted that birds acclimatized to cold temperatures have more plumage than birds which are heat acclimatized (West, 1962; Coulombe, 1970). They may also move their feathers rapidly (Hutchinson, 1954; McFarland and Budgell, 1970), through pilomotor activity, and alter blood flow. Plumage resistance to heat flow is also altered by wind velocity. An increase in wind velocity up to approximately 4 mph decreases plumage insulation (Evans and Moen, 1975; Robinson et al., 1976). In the sharp-tailed grouse however, feather orientation has little effect on thermal conductance at different wind speeds (Evans and Moen, 1975).

The skin temperature of feathered areas is less labile to changes in ambient temperature than the temperature of unfeathered extremities. Richards (1971) found that when the ambient temperature of the chicken was increased from 20 to 40C, the skin temperature of the feathered areas varied

from 2 to 5C whereas the unfeathered surface temperature varied 11 to 17C. These changes in skin temperature affect heat loss and indirectly alter metabolism. Hissa and Palokangas (1970) found that the winter-acclimatized, naked titmouse had a higher metabolic rate than the fully insulated animal.

The heat flow rate through plumage is not usually measured separately from that through the tissue, due to difficulties of measuring heat flow through each layer. Estimates of heat flow are made by one of two methods. One method involves a measurement of the cooling rate of an animal's body shortly after death (Herried and Kessel, 1967; Kleiber, 1972) which primarily assesses conductive heat flow through the tissue and plumage since there is no convective heat transfer in the dead animal. The other method estimates thermal conductance by evaluating the ratio between metabolic heat production and the difference between core and ambient temperature in the live bird (Kendeigh, 1970). This measures heat transferred by net conductive, convective, evaporative and radiant exchange.

Thermal conductance of the carcasses of birds, mammals and lizards increases exponentially with a decrease in body weight (Herried and Kessel, 1967). Kleiber (1972) concluded that basal metabolic rate of birds and mammals increased with the 3/4 power of body weight and heat conductance of their carcasses only increased with the 1/2 power of body weight. He suggested that this fact gives further

explanation of Bergmann's rule which states that large animals are favored for survival in cold environments.

Numerous estimates of thermal conductance for live birds indicate that it is lower in winter-acclimatized than in summer-acclimatized birds (Hart, 1962; Coulombe, 1970). In addition, there are rapid changes in thermal conductance which parallel those in ambient temperature. For some birds, thermal conductance decreases with a drop in ambient temperature, far below the lower critical temperature (West, 1962; Pinshow et al., 1976), while others show no change in thermal conductance below the lower critical temperature and only increase thermal conductance when heat stressed (Hudson and Brush, 1964; MacMillen et al., 1977). These studies show that adjustment of heat flow is used in the adult to maintain thermal balance when they are exposed to different ambient temperatures.

In young birds, sufficient thermal insulation is required before they can maintain homeothermy. The majority of the studies which have investigated the relationship of insulation to the development of thermoregulation have concentrated on either changes in plumage amount and/or whole body thermal conductance. Because of their size, it is difficult to measure heat transfer in the young bird.

Plumage growth is different whether the bird is precocial or altricial. The chicken is covered with down at hatching and is soon able to maintain a constant body temperature (Wekstein and Zolman, 1971). Body temperature

stability at the adult level is acheived in the precocial bird with the development of a complete feather covering (Whittow, 1976a). Altricial birds are naked at hatching and are not able to develop an effective level of body temperature control for the first 8 days after hatching (house sparrows-Seel, 1969; owls, flickers-Gardener, 1930; mourning doves-Breitenbach and Baskett, 1967; cactus wrens-Ricklefs and Hainesworth, 1968; grey-crowned rosy finches-Yarbrough, 1970). In some altricial birds, the development of homeothermy precedes the development of plumage (Dawson and Evans, 1957), whereas in others, the growth of feathers parallels the acquisition of homeothermy (Gotie and Knoll, 1973).

The development of resistance to cooling which generally parallels plumage growth is a primary factor in the development of homeothermy. In Japanese quail hatchlings, there is a 4-fold increase in plumage per unit surface area over the first 16 days after hatching (Spiers et al., 1974). It is in approximately this same time that the major decrease in body cooling rates occurs. McNabb and McNabb (1977b) demonstrated that the insulative capacity of skin-feather pelts from the Japanese quail increased 22% during the first 13 days after hatching. Young black-bellied tree ducks show a similiar decrease in body cooling rates for the first 10-12 days after hatching (Cain, 1972) while juvenile down is developing and its thermal insulation is increasing. Untergasser and Hayward (1972)

suggested that eider ducklings have a more rapid development of cold resistance than either mallards or scaups because of the superior insulative capacities of their plumage.

Thermal conductance in young birds appears to vary directly with ambient temperature (Dawson et al., 1972; Bernstein, 1973; Dawson et al., 1976; MacMillen et al., 1977). Dawson et al. (1972) suggested that the decrease in thermal conductance at low ambient temperatures might be due to the development of hypothermia in the young birds and consequently a reduction in the core-ambient temperature gradient. For most adults, there is little change in thermal conductance below the lower critical temperature.

Few studies have examined the cardiovascular response of young birds to different ambient temperatures. There is no information as to how this response affects body insulation. When bantam chicks are exposed to cold, there is a long-term change in heart size with no change in heart rate (Aulie, 1977). This suggests that there is an increase in stroke volume and cardiac output during cold exposure. At high temperatures, there is an increase in heart rate in the nestling ring-billed gull from 300 beats/min to 528 beats/min (Dawson et al., 1976) which may increase peripheral blood flow and facilitate heat loss.

VII. Shivering Thermogenesis

A mechanism by which birds increase heat production during cold exposure is by shivering thermogenesis or the generation of heat by the "increased contractile activity of skeletal muscles not involving voluntary movements and external work" (Bligh and Johnson, 1973). Adult mammals shiver as a means of increasing heat production when environmental temperature is below the animal's lower critical temperature. In the adult, inactive bird, shivering is the primary means for heat generation during cold exposure (grosbeaks, redpolls, grackles, crows-West, 1965; pigeons-Steen and Enger, 1957; willow ptarmigan, bantam-Aulie, 1976b; red-footed booby-Shallenberger et al., 1974; titmouse-Hissa and Palokangas, 1970) which may increase metabolic rate 3-5 times above the basal level (Lustick et al., 1978). There may be an inverse relationship between shivering activity and ambient temperature below the lower critical temperature (Steen and Enger, 1957; Hart, 1962; West, 1965).

A large portion of the body mass of flying birds is in their pectoral muscles (Calder and King, 1974). Both the frequency and amplitude of pectoral muscle movement increases during shivering which produces an increase in their temperature (Steen and Enger, 1957). Aulie (1976b) noted that shivering activity and heart rate are related for both willow ptarmigans and bantams. It was suggested that their functional relationship increases the effectiveness of

heat distribution in the bird and would explain the rise in subcutaneous and cloacal temperatures seen during shivering (Aulie, 1976b).

There are different responses in shivering activity when the bird is acclimatized or acclimated to cold temperatures. Hart (1962) found no seasonal changes in the shivering activity of pigeons, however, El-Halawani et al., (1970) noted that leghorns decreased muscle electrical activity when their cold acclimation time was increased. They suggested that the increased cold exposure caused the development of nonshivering, thermogenic mechanisms, producing less reliance on shivering thermogenesis.

The development of homeothermy in birds is correlated with the development of shivering ability (Calder and King, 1974). In some species, shivering activity may be seen in the embryo. The ring-necked pheasant embryo may shiver as early as 9 days of incubation when exposed to 37.2C (Odum, 1942) and the duck embryo shivers at 37.5C toward the end of incubation (Romanoff, 1941). Oppenheim et al. (1975) noted that the rate of neuromuscular activity in the chick embryo at 15 and 20 days of incubation was altered when the environmental temperature was not equal to the incubation temperature.

Shivering activity in the hatchling has been detected as early as 1 day in the willow ptarmigan and willow grouse (Myhre et al., 1975; Aulie, 1976a). Even with shivering at this age, cloacal temperature declines with minor cold

stress. Pronounced shivering appears in many birds between 3-7 days after hatching (house wren, chickadee-Odum, 1942; mountain white-crowned sparrows-Morton and Carey, 1971; domestic chicks-Randall, 1943; mourning doves-Breitenbach and Baskett, 1967) whereas others show no signs of intensive shivering until 1-2 weeks after hatching (ring-billed gulls-Dawson et al., 1976).

Shivering activity in some nestlings appears to increase with a decrease in body temperature (Hudson et al., 1974) and decrease in others with a drop in body temperature (Aulie, 1976a). In addition, shivering in some nestlings may be continuous (Hudson et al., 1974) or intermittent (Odum, 1942) at low ambient temperatures. This difference is also seen in some adults with shivering being intermittent (willow ptarmigan) or continuously (bantam) (Aulie, 1976b) during exposure to cold.

It is generally agreed that the shivering response in nestlings increases with body size (Bartholomew, 1966; Aulie, 1976a). Aulie (1976a) attributes this to pectoral muscle mass increasing at a faster rate than the rest of the body (1.8% body weight on day 3 to 11% body weight on day 12), and suggests that it is the larger muscle mass which produces an increase in frequency and amplitude of muscle tremor.

VIII. Nonshivering Thermogenesis

Nonshivering thermogenesis is defined as heat production which is not related to the involuntary contraction of striated muscle. In some mammals, a large portion of their total heat production during cold exposure is by nonshivering thermogenesis (Dawkin and Hull, 1965; Horowitz et al., 1971). This heat is primarily generated by brown adipose tissue which is stimulated by norepinephrine released from sites of sympathetic innervation. In addition, norepinephrine stimulates lipolysis and fatty acid release from the brown adipose tissue (Hull and Smales, 1978). Thermogenesis by brown adipose tissue in cold-acclimated mammals contributes only a small portion of the nonshivering heat production (Hull and Smales, 1978). The additional heat production may be contributed by viscera and muscle metabolism in the cold-acclimated mammal (You and Sellers, 1951; Sellers et al., 1954; Weiss, 1954).

In newborn mammals, nonshivering thermogenesis is the major source of heat production (Carlson, 1969; Smith and Horowitz, 1969) and brown adipose tissue is the primary site of nonshivering thermogenesis (Hull and Smales, 1978). With development, there is a gradual decrease in nonshivering thermogenesis which is replaced by shivering thermogenesis.

There is little evidence for the presence of nonshivering thermogenesis in birds (West, 1965). Hart (1962) noted that when pigeons were injected with curare to inhibit shivering, there was no thermogenic response to

either cold or to norepinephrine injection. Chaffee et al. (1963) reported that when norepinephrine was injected into chickens acclimated to 1C for 3 months, there was no change in oxygen consumption nor an increase in thermogenesis. Norepinephrine, injected into the titmouse, produced a significant increase in plasma free fatty acids, stimulated hepatic glycolysis, or increased metabolic rate (Hissa and Palokangas, 1970). Although the circulating levels of norepinephrine and epinephrine are higher in cold exposed chickens than in controls (Yo-Chong and Sturkie, 1968), norepinephrine does not stimulate nonshivering thermogenesis in birds as it does in mammals.

Other investigators have found that nonshivering thermogenesis may be present under certain conditions in the adult fowl. El-Halawani et al. (1970) noted that with prolonged cold acclimation, adult fowl increased oxygen consumption and decreased shivering activity, indicating a greater dependance on nonshivering mechanisms for heat production. They also found that after adrenalectomy, muscle electrical activity completely disappeared in both cold and non-acclimated birds, with the oxygen consumption of non-acclimated birds being drastically lower than that of non-adrenalectomized, non-acclimated birds. This suggested that catecholamines might play a role in nonshivering thermogenesis. When propranolol, a B-adrenergic blocker, was injected into adult pigeons, both the calorigenic and hyperthermic effects of norepinephrine were prevented

(Pyornila et al., 1976). Injections of propranolol into cold exposed quail produced a drop in both body temperature and oxygen consumption (Freeman, 1970). Sturkie et al. (1970) suggested that this effect might be due to a decrease in heart rate rather than directly affecting sympathetic activation of nonshivering thermogenesis. However, Arieli et al. (1978) demonstrated in the adult fowl that the depressive effect of propranolol on oxygen consumption was independant of the reduced heart rate. This suggests that nonshivering thermogenesis is present in the adult fowl.

There is conflicting evidence for nonshivering thermogenesis in the young bird. No brown adipose tissue has yet been found in young birds (Freeman, 1967; Johnston, 1971). Mammalian sympathetic activators, norepinephrine and epinephrine, have been injected into chicks (Wekstein and Zolman, 1969) and blackhead gulls (Palokangas and Hissa, 1971) with no effect. Other investigators have found that either intravenous (Allen and Marley, 1967) or intrahypothalamic (Marley and Stephenson, 1975) injections of norepinephrine into young chicks produced decreases in both skin and core temperatures, suggesting that norepinephrine might inhibit heat production and/or facilitate heat loss in chicks.

Evidence for nonshivering thermogenesis in young birds is not conclusive. Freeman (1966) demonstrated that norepinephrine injected into the neonate chick produced a

small rise in oxygen consumption and a decrease in both muscle and liver carbohydrate content. He also found an increase in plasma free fatty acid levels with norepinephrine injections (Freeman, 1967). The injection of propranolol into the newly hatched cold-exposed chick caused a steady decrease in cloacal temperature and oxygen consumption (Wekstein and Zolman, 1968).

IX. Thyroid Activity

Thyroid gland activity is different at different ambient temperatures and affects the response of animals exposed to these temperatures. In both birds and mammals, there is an increase in thyroid activity with a decrease in ambient temperature (Mills, 1918; Dempsey and Astwood, 1943; Reineke and Turner, 1945; Hoffman and Shaffner, 1950; Stahl and Turner, 1961; MacFarland et al., 1966; Hendrich and Turner, 1967; Harclerode and Dropp, 1967; Raitt, 1968; Chaffee and Roberts, 1971), although the thyroid response of the bird to low ambient temperatures is a slow process (Stahl et al., 1961). An increase in thyroid hormone production in birds and mammals produces an increase in metabolic rate and a reduced drop in metabolism and body temperature at cold temperatures (Reineke et al., 1945; Sulman and Perek, 1947; Swanson, 1957; Washburn et al., 1962; Steele and Wekstein, 1972), suggesting that thyroid hormones are important in the maintenance of homeothermy.

The predominant thyroid hormones in birds and mammals

are thyroxine (T_4) and triiodothyronine (T_3). It is unclear which of these is more important to the animal. Thyroxine is a potent stimulator of metabolism (Raheja and Snedecor, 1970) and, in some cases, is more important than triiodothyronine (Newcomer and Barret, 1960; Singh et al., 1968a), however T_3 is 2-4 times more active than T_4 (Slivastava and Turner, 1967b; Ringer, 1976; Bernal and Refetoff, 1977; Oishi and Konishi, 1978). There is, however, considerable peripheral conversion of T_4 to T_3 (Braverman et al., 1970; Astier and Newcomer, 1978; Campbell and Leatherland, 1979). Several investigators suggest that T_4 is only a prohormone and that thyroid activity is primarily related to T_3 activity (Oppenheimer et al., 1972) especially at low ambient temperatures (Oishi and Konishi, 1978).

Thyroid activity in birds may display diurnal and annual rhythms. In the juvenile bird, T_3 and T_4 plasma levels fluctuate daily with a peak T_3 8-12 hours after the start of the light period and a T_4 peak during the dark period (Newcomer, 1974; Klandorf et al., 1978). In addition there are annual rhythms in thyroid activity in birds (Hohn, 1949; Raitt, 1968; Jallageas et al., 1978). These fluctuations are often correlated with molting behavior and/or changes in ambient temperature.

Thyroid activity may not only influence metabolism and body temperature, but may also affect other body functions which indirectly relate to thermoregulation. Molting

behavior in some birds is effected by an increase in thyroid activity. Summer molts in ducks (Astier et al., 1970; Jallageas et al., 1978), Gambel's quail (Raitt, 1968) and white-tailed ptarmigan (Hohn and Braun, 1977) occur with an increase in thyroid activity, however, Sulman and Perek (1947) noted that feeding thiouracil (TU) to chickens did not prevent molting. They indicated that molting may stimulate thyroid activity. Ringer (1976) suggested that the differences in the relationship of thyroid activity to molting among species could be due to differences between passerine and nonpasserine birds.

Thyroid hormones may also produce daily changes in heart rate. Shimada and Oshima (1973) found that T_4 increased heart rate in the chicken 2 hours after its administration. They proposed that the hormone could modify the autonomic nervous system and decrease vagal tone. Klandorf et al. (1978) noted that daily heart rate increases in juveniles corresponded with increases in plasma T_3 levels. The increases in heart rate could increase stroke volume and cardiac output and facilitate body heat distribution.

Thyroid hormone production begins in the chick on day 10 of incubation (Trunnell and Wade, 1955; Thommes and Hylka, 1977). The plasma levels of T_4, T_3, and reverse T_3 increase from day 10 to hatching (Thommes and Hulka, 1977). Thyroid iodine content increases in the chick embryo on days 12-13 of incubation (Daugeras and Lachiver, 1972) and 7-4

days before hatching in the Japanese quail (McNabb et al., 1972). McNabb et al. (1972) suggested that the thyroid gland's initial function is production and storage of the hormone, rather than its release. In both species, there is an abrupt decrease in thyroidal iodine content shortly after hatching and plasma thyroid hormone levels increase. King et al. (1977) found that T_3 concentration increased from 11 ng% in the 17 day embryo to 330 ng% at hatching, then decreased to one-half this level over the first day after hatching. Others note that thyroid activity (Spiers et al., 1974) and plasma hormone levels (Davison, 1976; Thommes and Hylka, 1977) peak on day 1 after hatching. Davison (1976) suggested that the rise in thyroid hormone levels at this time could be due to an increased release of TSH and/or cold stress to the hatchling on emerging from the shell. The increase in thyroid hormone levels at hatching corresponds with the increase in metabolism seen at this time (Balaban and Hill, 1971), both of which are required for the bird to hatch.

A similiar increase in thyroid activity occurs in the neonatal mammal shortly after birth (human-Abuid et al., 1973; Erenberg et al., 1974; Simila et al., 1975; calf-Nathanielsz and Thomas, 1973). In the neonatal rat, thyroid activity is low at birth and does not increase until several days later (Beltz and Reineke, 1968; Dussault and Labrie, 1975). As in the bird, this increase is attributed to a rise in TSH levels (Abuid et al., 1973; Erenberg et

al., 1974; Simila et al., 1975) brought about by extrauterine cooling (Erenberg et al., 1974). In mammals, the T_3 and T_4 plasma levels may remain elevated above adult levels for as long as 12 1/4 years in humans (Stubbe et al., 1978) and 60 days in the rat (Beltz and Reineke, 1968). In the calf, the hormone levels may decrease almost immediately after its rise on day one (Nathanielsz and Thomas, 1973). Thyroid hormone levels in the chick also decrease shortly after hatching (Davison, 1976). Thyroid secretion rate in chicks is highest at two weeks of age (Tanabe, 1965) and thyroid growth may continue for 100-120 days after hatching (Breneman, 1954).

Thyroid hormones are required after hatching for thermoregulation and growth in the neonate. Freeman (1970) found that injection of T_3 or T_4 into the neonate fowl produced an increase in rectal temperature within 15 minutes and reduced hypothermia on cold exposure. Spiers et al. (1974) noted that the development of thyroid function parallels the development of thermoregulatory ability in the Japanese quail. Thyroid hormones increase the metabolic rates of neonatal chicks (Singh et al., 1968a) and possibly function as a source of increased heat production in nestling vesper sparrows (Dawson and Evans, 1960). Bobek et al. (1977) noted that the maximum oxygen consumption in the young chick at its thermoneutral temperature occurred during the first to second weeks after hatching. This increase in metabolism was correlated with increased T_3 plasma levels.

The treatment of neonatal chicks with thiouracil and the resulting reduction in thyroid activity is accompanied by a faster fall in body temperature on cold exposure (Freeman, 1971c) than for control birds. There is also a reduction in the growth of chick hatchlings (Mellen and Hill, 1953; Snedecor and Camyre, 1966; Marks and Lepore, 1968; Singh et al., 1968a; King, 1969; Raheja and Snedecor, 1970; King and King, 1975), and a decrease in muscle weight (King and King, 1976) when thyroid activity is reduced due to a decrease in food consumption (King, 1969; Raheja and Snedecor, 1970). Liver size and hepatic glycogen levels increase with reduced thyroid activity (Snedecor and King, 1964; Snedecor and Camyre, 1966; Snedecor, 1968; King, 1969; Raheja and Snedecor, 1970; King and King, 1976), indicating reduced metabolism of carbohydrate stores. This demonstrates that thyroid hormones are required for growth and food utilization in the young bird.

Immature birds and mammals are able to respond to cold exposure with an increase in thyroid activity. Young piglets increase T_4 secretion during cold exposure (Evans and Ingram, 1977). Young chicks exposed to low temperatures also increase thyroid hormone secretion (Hoffman and Shaffner, 1950; Kuhn and Neuman, 1978) and display a decrease in T_4 half-life (May et al., 1974). The increase in thyroid activity enables the young animal to increase metabolic heat production and maintain a constant body temperature.

X. Evaporative Heat Loss

Birds rely heavily on evaporative water loss for thermal balance. In adult birds, there is a small increase in evaporative water loss with an increase in ambient temperature (Kendeigh, 1944; Bartholomew et al., 1962; Calder and King, 1974; Baudinette et al., 1976) to the upper critical temperature limit. Once ambient temperature reaches a bird's upper critical temperature, there may be a 5-fold increase in evaporative water loss (Dawson, 1958; Marder, 1973; Pinshow et al., 1976). Generally the increase in evaporative water loss does not appear until after the animal's body temperature has risen slightly (Calder, 1964; Richards, 1970).

Both cutaneous and respiratory evaporation are avenues of heat loss in the adult birds. In thermoneutrality, cutaneous water loss contributes between 42-84% of the evaporative heat loss (Calder and King, 1974) and plays a major thermoregulatory role in some birds during flight when there is a large increase in heat production (Smith and Suthers, 1969).

Since birds do not have sweat or sebaceous glands (Jenkinson and Blackburn, 1968), water must pass through the avian skin by diffusion to evaporate at the skin surface or be absorbed by the plumage. Plumage may serve to store water and delay evaporative cooling effects (Calder and King, 1974).

There is increased reliance on respiratory evaporative

heat loss at high ambient temperatures which may increase by panting (Brush, 1965; Hudson and Kimzey, 1966; Spellerberg, 1969; MacMillen et al., 1977) and by gular fluttering (Bartholomew, 1953; Brush, 1965). During panting, the bird increases its respiratory frequency and respiratory minute volume, but decreases tidal volume (Whittow, 1976a). Heat loss by panting may account for 70% of the metabolic heat production (Mugaas and Templeton, 1970) if the breathing rate reaches the resonant frequency of the animal's respiratory system (Calder and King, 1974). At this level, less energy is required for panting and evaporative water loss. Some birds use less energy by gular fluttering (Whittow, 1976a) which involves rapid movements of the hyoid apparatus in the floor of the mouth. This body area is well perfused with blood and mobile. With gular fluttering, increases in evaporative water loss both by evaporation and by forced convection occur at low energy cost. The burrowing owl (Coulombe, 1970) and poorwill (Bartholomew et al., 1962) are able to evaporate more than 135% of its metabolic heat production by gular fluttering.

Evaporative cooling in young birds occurs soon after hatching (cattle egrets-Hudson et al., 1970; wrens-Kendeigh, 1939; Ricklefs and Hainsworth, 1968; chicken-Randall, 1943). Usually the weight-specific water loss is higher in hatchlings than in adults (Medway and Kare, 1957) and decreases with age, as in the Chinese painted quail for which a 38-53% decrease in cutaneous water loss occurs over

the first four weeks after hatching (Bernstein, 1971). Bernstein (1969) noted that as much as 70% of the heat loss at an ambient temperature of 25C by painted quail hatchlings was due to cutaneous evaporation. He attributed the high cutaneous water loss to high skin water permeability, sparse plumage, the establishment of large temperature and water vapor pressure gradients across the skin along with poor control of peripheral circulation. These allow both peripheral blood flow and skin water content to increase (Bernstein, 1971). This increases cutaneous water loss in the hatchling. Recently, McNabb and McNabb (1977b) noted that the skin permeability of the Japanese quail decreased with age to the adult level at 13 days of age. This is nearly the age at which the Japanese quail attains adult homeothermy (Spiers et al., 1974).

Young birds can increase evaporative water loss 5-fold at high ambient temperatures (Dawson et al., 1976) which may begin at a lower body temperature in young birds than in adults (Whittow, 1976a). As in adults, the increase in evaporative water loss is by panting (Howell and Bartholomew, 1962; Breitenbach and Baskett, 1967; Morton and Carey, 1971; Dawson et al., 1972; Hudson et al., 1974; Myhre et al., 1975; O'Conner, 1975) and gular fluttering (Bartholomew, 1953; Hudson et al., 1974).

Increases in heat loss for young birds occurs before they maintain a constant body temperature, suggesting that thermolytic mechanisms develop before the thermogenic

mechanisms (Dawson et al., 1976; Gotie and Knoll, 1973). This could produce high levels of thermal conductance (core to ambient) at elevated air temperatures.

XI. Radiant Heat Exchange

Any object with a temperature above absolute zero radiates heat proportional to the fourth power of its absolute temperature (Calder and King, 1974). Electromagnetic radiation, with wavelengths from 0.38 to 0.78um include visible light and those from 0.78 to 100um include the infrared portion of the spectrum. When electromagnetic radiation reaches an object it is reflected and/or absorbed. The skin and plumage color of birds is a major determinant of visible radiant energy absorbed, with dark-colored objects absorbing more visible radiation than light-colored objects. However, birds act as "blackbodies" in the infrared portion of the electromagnetic spectrum (Hammel, 1956), as do all animals.

When energy from visible solar radiation is absorbed by a surface (i.e. skin, fur, plumage, clothing) it can be broken down into infrared energy. In birds, this conversion of absorbed visible radiant energy is successful in raising the feather surface temperature (Heppner, 1969; Heppner, 1970; Lustick et al., 1978). This increase reduces the skin-surface thermal gradient and lowers heat loss, which reduces the requirement for heat production to maintain a constant body temperature. This is supported by the

evidence that dark-colored birds require less energy to maintain normal body temperature than light-colored birds, when exposed to equal rates of solar radiant energy gain (Hamilton and Heppner, 1967; Lustick, 1969; Heppner, 1970).

Radiant energy sources may be used by birds for heat gain when there is a fall in ambient temperature. White-crowned sparrows (De Jong, 1976) select environments with more intense thermal radiation at low ambient temperatures and those irradiated at cold temperatures have lower metabolic rates than those which do not receive radiant energy. Roadrunners can save 551 calories per hour when exposed to radiant energy (Ohmart and Lasiewski, 1971).

The role of radiant energy in the development of thermoregulation has received limited investigation for birds, although parental shading of young is important in preventing overheating. Body temperature of the young increases shortly after the parent leaves the nest (Bartholomew and Dawson, 1954; Hudson et al., 1974).

XII. Behavioral Thermoregulation

The ability of an animal to maintain a constant body temperature in different environments depends on physical, physiological and behavioral factors. In its natural environment, the bird is often able to adjust behaviorally its microclimate to reduce thermal stress.

The adult bird has many behavioral mechanisms for the maintenance of a constant body temperature at either high or

low ambient temperatures, one of which is migration. Birds also seek a shaded area during exposure to high temperatures (Bartholomew and Cade, 1957). Small birds show no seasonal alteration in metabolic response or changes in insulation (Delane and Hayward, 1975), but rely on adjusting their activity. Some decrease heat loss during cold exposure by behavioral techniques which reduces the exposed surface area and increases insulation. These include adopting a spherical shape (Steen, 1958), huddling (Steen, 1958), coveying (Case, 1973) and fluffing out the feathers (Bartholomew and Dawson, 1954; Horowitz et al., 1978).

The head and legs of most birds are important areas for heat exchange due to their low thermal insulation and their high vascularization. During cold exposure, many adult birds tuck their heads under their wings (Dawson and Hudson, 1970; Horowitz et al., 1978) and/or sit on their feet (Deighton and Hutchinson, 1940; Scholander et al., 1950a; Bartholomew and Dawson, 1954; Horowitz et al., 1978) to reduce body surface area. At high ambient temperatures, these body regions are extended to increase heat loss (Steen and Steen, 1965; Dawson and Hudson, 1970; Whittow, 1976a). Other birds wet these areas during heat stress to increase evaporative heat loss. Chickens at high temperatures will spread water over the highly vascularized comb and wattles (Wilson, 1949). Several species of birds, which have long legs (i.e. American wood-stork, turkey vulture, black vulture), increase heat loss by wetting the legs with urine

(Calder and King, 1974).

Behavioral thermoregulation first appears in the embryonic stage of development. Purdue (1976) found that egg temperature of snowy plovers was maintained constant by parental incubation behavior which increased at ambient temperatures between 41-45C to reduce overheating the eggs, but was reduced between 31-40C.

After hatching, the chick selects an environment which is not thermally stressful (Ogilvie, 1970). In a thermalgradient, the newly hatched maintains a preferred body temperature lower than that of the adult (Poczopko, 1967; Spiers et al., 1974; Myhre et al., 1975; Myhre, 1978). The bird selects a lower ambient temperature as it ages due to the increase in its thermoregulatory ability.

The two, primary, behavioral mechanisms used for hatchling thermoregulation are huddling and brooding by parents. Huddling in hatchlings reduces heat loss (chicks-Kleiber and Winchester, 1933; Barott et al., 1936; pigeons-Riddle et al., 1932; cattle egrets-Hudson et al., 1974; laughing gulls-Dawson et al., 1972) and may account for a 15% reduction in metabolic heat production as well as reduce energy required for homeothermy during exposures below the lower critical temperature.

Brooding behavior of parents for offspring is often required for survival of the young (Cain, 1972) as well as for maintenance of homeothermy in hatchlings which lack thermoregulatory ability (Caldwell, 1973) or which are

exposed to different ambient temperatures (Yarbrough, 1970; Dawson et al., 1976). In some birds, brooding behavior is more important than shivering in maintaining a constant, high body temperature (Aulie and Moen, 1975). An increase in brood size produces a drop in metabolic rate due to a decrease in the surface area-to-volume ratio (Mertens, 1969). With the physiological development of homeothermy in the bird, there is a reduction in the time the adult spends brooding its young (Morton and Carey, 1971; Dawson et al., 1976; Dunn, 1976; Austin and Ricklefs, 1977; Boggs et al., 1977). Brooding behavior is not only required during exposure to low ambient temperatures, but is also necessary to prevent overheating, as when the adult shades the young from intense solar radiation (Bartholomew, 1953; Bartholomew and Dawson, 1954; Hudson et al., 1974) or by movement of young in and out of the parental shade (Dunn, 1976).

XIII. Bobwhite

The bobwhite is classified as:

Order: Galliformes

Family: Odontophoridae - American quails

Genus: Colinus

Species: virginianus

The earliest known quail of the genus Colinus lived in Kansas during the Pliocene Epoch, approximately 1 million years ago (Rosene, 1969). The present day Bobwhite first appeared during the Pleistocene Epoch (15,000 years B.P.).

The bobwhite is now found in North and Central America. In North America, there are 5 subspecies of Colinus virginianus, which range as far north as Michigan and New York, as far south as Florida and as far west as Nebraska (Rosene, 1969).

Adult quail usually raise 2 broods of young per season (Bent, 1932). Each clutch contains approximately 14 eggs which are incubated by both male and female adults during the 23 day incubation period (Stoddard, 1936). Chicks are led away from the nest within 4-5 hours after hatching (Stoddard, 1936) to avoid predators, however, they are brooded over constantly by the parents for the first two weeks after hatching or until they reach a size when the adult cannot cover them. At 3-4 weeks of age, the juveniles form disklike coveys similiar to those of the adults during the winter (Rosene, 1969). The chicks are never fed by the parents during the brooding period and must find insects themselves.

A primary factor in the development of homeothermy for the quail is the quantity and quality of plumage. The young quail's plumage changes drastically over the first 4-5 weeks after hatching. Quail are covered totally by down during the first 3-4 days when pin feathers start to appear on the wings. By days 5-7, feather shafts appear along feather tracts located on the breast, back and sides (Rosene, 1969). Also at 5-7 days after hatching, some feathers start to unsheath (Lyon, 1962). By 2 weeks of age, the juvenile

scapulars and wing feathers are long enough to offer protection from light rains, and at 3 weeks the juvenile plumage predominates (Stoddard, 1936). The wing feathers develop rapidly over the first 4 weeks after hatching and by 28 days they can be used to cover the body for protection from cold, wind or rain. At the same time, the first molt begins. The wing feathers begin to be replaced at 28 days of age by a second coat. The complete body molt does not occur until 7 weeks of age (Lyon, 1962). Young quail never completely molt at any time in their development, but only partially molt. The second feather coat is stiffer and less mottled than the first (Rosene, 1969). At 35 days of age, the quail is able to survive extreme weather conditions without being brooded by its parents and may roost with the adults in the covey formation (Stoddard, 1936). The bobwhite has almost an entire adult plumage by 100 days of age, except for some juvenile plumage still present on the back of the head. The adult molts twice a year with a complete molt in late summer or fall and a partial molt of head and throat in the spring (Lyon, 1962).

Stoddard (1936) noted that there were two growth phases in the bobwhite. The daily weight tripled between day 10 and day 19, advancing from .50 g/day to 1.50 g/day. The growth rate increases again at 43 days to 1.75 g/day.

Bobwhite gather together in covey formation during cold weather. In forming the covey, they force their bodies close together with tails sticking upward in the center of

the disk. The reduction in the surface area for evaporative cooling and the reduced temperature gradient for radiative and convective heat loss function to reduce heat loss from the group. Their heads stick out of the covey to allow for rapid flight when faced with danger. Case (1973) found that existence energy was greater for individual quail at 5C than for quail in covey formation at 5C. However, at temperatures above 5C there was greater energy utilization for quail in coveys than for individuals. Covey formation is an effective mechanism for reducing energy loss from the quail only at 5C or below.

MATERIALS AND METHODS

I. Animals

A. Housing

Bobwhite (Colinus virginianus) eggs obtained from the Michigan State University Poultry Farm were incubated for 23 days at 39 C in Single-Stage Jamesway 252 Incubators and after hatching, the quail were placed in metal brooder cages located in the Poultry Department vivarium. A temperature gradient from 40C to a room temperature of approximately 25C was maintained within each brooder. Adult quail (1 to 3 years of age) were housed in wire cages, two birds per cage, and maintained at room temperature. The average vivarium room temperature was 25C±3C from summer to winter months (Appendix 1 and 2). A 16 hour light:8 hour dark photoperiod was maintained in the vivarium throughout the experimental period.

B. Diet

All birds received food and water ad libitum. Immature bobwhite, prior to January 31, 1978, were fed MSU 72-15 Quail Starter Diet (Appendix 3) and the adults were fed MSU 72-16 Quail Breeder Diet (Appendix 3) during the growth and thyroid hormone studies. In order to eliminate any possible

differences between the adult and immature quail due to dietary influences, all quail were fed the MSU 72-15 Quail Starter Diet beginning on January 31, 1978 (Appendix 4). The stress effect of the Starter Diet on the adult quail was tested by measuring the differences between the body and adrenal masses of control and experimental adult quail (Appendix 4). There were no significant differences between the two groups, indicating that the Starter Diet did not abnormally stress the adult quail.

II. Growth Rate

Bobwhite were placed in brooders on the day of hatching. Quail Starter Diet (MSU 72-15) was provided in plastic feeders (depth, 5cm). A movable section of hardware cloth (1/4 inch mesh) was placed on top of the food to prevent the quail from scratching it out of the feeder. Quail body mass was measured from 1-65 days after hatching. Each bird was removed from the brooder between 5-10 pm and weighed individually on a Mettler P1210 Toploader Balance (Mettler Instrument Corporation, Princeton, New Jersey) to the nearest 0.01g.

III. Plumage

The amount of plumage on the adult and immature quail at 1, 3, 6, 10, 14, 18, 25, 45 and 65 days after hatching was measured by plucking the freshly killed (cervical dislocation) bird and weighing the plumage to the nearest

milligram on a Mettler Preweigh Balance (Mettler Instrument Corporation, Princeton, New Jersey).

The amount of plumage per unit body mass was calculated by dividing each bird's plumage weight by its body weight before plumage removal. Down and juvenile feather location was noted for the transitional period when down is being replaced by juvenile feathers (1-18 days after hatching). Black and white feathers were taken from adult and immature quail (1, 3, 6, 10, 14, 18, 25, 45, 65 days of age) to provide an indication of body size and general plumage distribution.

IV. Thermoregulatory Measurements

A. General Procedure

The thermoregulatory responses of adult and immature quail (1, 3, 6, 10, 14, 18, 25, 45, 65 days of age) was examined as they were exposed to ambient temperatures of 10, 15, 20, 25, 30 and 35C. Each bird was individually exposed in a water-jacketed, metabolic chamber to a selected ambient temperature (Figure 1). Effluent air was analyzed for oxygen (P_{O_2}), carbon dioxide (P_{CO_2}) and ambient relative humidity (%rh). Internal body temperature was recorded during the run.

Quail, 14 days of age and older, wore lightweight blinders to reduce their activity and their awareness of disturbances from their surroundings. A paper towel was placed around the chamber when birds younger than 14 days of

Figure 1. Apparatus for thermoregulation studies.

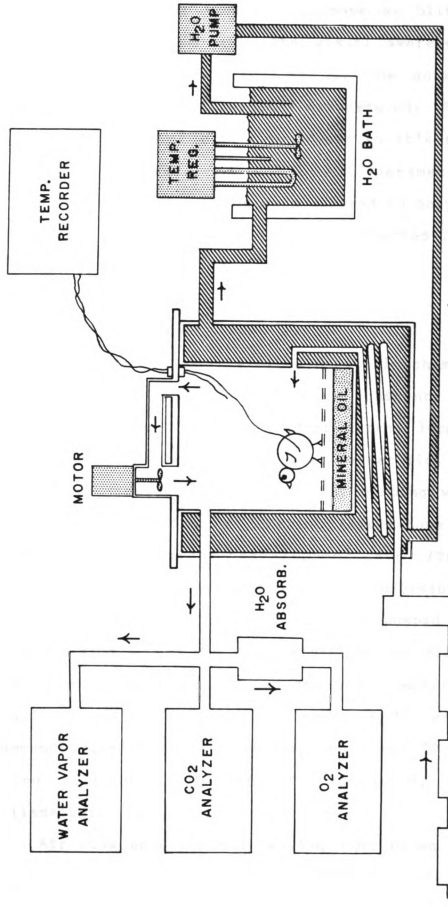

TEMP. RECORDER
TEMP. REG.
H_2O PUMP
H_2O BATH
MOTOR
MINERAL OIL
H_2O ABSORB.
FLOWMETER
WATER VAPOR ANALYZER
CO_2 ANALYZER
O_2 ANALYZER
AIR PUMP
H_2O ABSORB.
CO_2 ABSORB.

Figure 1

age were tested for the same purpose as blinders on the older birds. By reducing the visual awareness of their surroundings, the time required for the animal to reach steady-state levels of response was reduced. Each bird was allowed a minimum of 1 hour to adjust to it's surroundings, with no data recorded until all parameters reached steady-state levels. Birds were exposed to only one ambient temperature daily and they were not retested for a minimum of three days.

B. Metabolic Chamber

A water-jacketed, plexiglas metabolic chamber (Fig. 1) was used to maintain air temperature constant. The chamber had an inner air space (id, 14cm; depth, 16cm) which was surrounded by a water-filled, outer jacket (id, 21cm; depth, 22cm). Chamber air was adjusted by pumping water through the outer jacket from a constant temperature bath, using either an immersion heater-pump unit (Techne Inc., Princeton, New Jersey) or a vertical immersion pump (Cole Palmer, Chicago, Illinois). Air was pumped through the chamber using a Dyna-Vac Pump (Fisher Scientific, Pittsburg, Pennsylvania) at the inflow of the unit. Water was removed from the inflow air using a tube of "Drierite" (W. A. Hammond Drierite Company, Xenia, Ohio) and CO_2 was removed using a tube of "Ascarite" (Arthur H. Thomas Co., Philadelphia, Pa.).

Air flow entering and leaving (not shown on Figure 1,

but located at air exit from chamber) the chamber was monitored with rotametric flowmeters (Scientific Glass Apparatus Co., Inc., Bloomfield, New Jersey). Flowmeters were calibrated by a water-displacement technique (Appendix 5). Flowrates ranged from 70ml/min to 800ml/min and were adjusted during each experiment to maintain chamber PO_2 above 19%, PCO_2 below 1.5% and %rh below 50%.

Dry air passed through 1/4 inch diameter copper tubing in the chamber's water jacket before entering the inner air space. The chamber lid was sealed to the chamber wall (thickness, 3.5cm) using high vacuum silicone grease (Dow Corning Corp., Midland, Michigan).

A small, 12 volt DC fan (Pittman Corporation, Sellersville, Pennsylvania) in the chamber lid (Figure 1) circulated air in the chamber. Thermal profiles for the chamber at different air temperatures (11.45, 20.67, 29.00, 38.90C) are shown in Appendix 6.

A platform of 1/4 inch hardware cloth was placed 2.5cm from the bottom of the inner air chamber. Mineral oil, under the hardware cloth, covered fecal matter deposited during the experiment.

C. Oxygen Analysis

A Beckman, Model F3, Oxygen Analyzer (Beckman Instruments, Inc., Fullerton, California - Appendix 7) was used to measure the oxygen content of the dried, effluent, chamber air to the nearest .01%. The detection range for

the analyzer was set at 14-21%. The analyzer was calibrated daily and periodically checked on the day of an experiment using dry, room air. Voltage output from the analyzer was recorded on a Moseley Model 175Ø1 Plug-In Unit connected to a Moseley Model 71ØØBM Strip Chart Recorder (Hewlett-Packard Corp., Pasadena, California).

D. Carbon Dioxide Analysis

Carbon dioxide content of the chamber effluent air was measured to the nearest .Ø1% by a Beckman Medical Gas Analyzer Model LB-2 (Beckman Instruments, Inc., Anaheim, California - Appendix 8) and was read from the digital display meter. Instrument baseline and gain adjustments were made daily. Dry, room air was pumped through the analyzer at a flowrate used during the experiment and the zero control was adjusted to obtain a panel reading of Ø.Ø3%CO_2. Gain calibration was performed by passing a calibration gas through the analyzer and adjusting the gain control to obtain a %CO_2 reading of the standard gas sample. The calibration gas ranged from 1 to 4% and was analyzed using a Haldane apparatus.

E. Evaporative Water Loss

A Hygrodynamics Relative Humidity Transducer was used to measure the percent relative humidity (%rh) of the effluent air. Voltage output from the transducer was recorded on a Moseley Strip Chart Recorder to provide a

continuous record. Recorder sensitivity was adjusted before each experiment by first setting the recorder sensitivity to 2 volts and then pumping dry, room air through the transducer while the baseline was adjusted. A calibration, crystalline rod (Appendix 9) was then inserted into the transducer to simulate 100%rh and the recorder pen was adjusted, using the fine sensitivity adjustment, to yield a deflection of 25cm. This calibration procedure is recommended by the manufacture. Once the recorder sensitivity was adjusted, the %rh was read directly from the chart record, using the calibration curve (Appendix 9) for the appropriate sensitivity setting.

F. Temperature Measurements

Internal body temperature (T_b) and chamber air temperature (T_a) were measured using 40-gauge copper-constantan thermocouples (Appendix 10), referenced to an ice-water bath. All temperatures were recorded on a Speedomax W multipoint recorder (Leeds and Northrup, Model AZAR-H, Philadelphia, Pa.) and temperature values calculated using the calibration curve for 40-gauge thermocouples (Appendix 10). Chamber air temperature was measured by a thermocouple which was suspended approximately 2cm from the lid (Figure 1). It did not touch the animal or the chamber wall during measurements.

Internal body temperature measurements were made using a thermocouple inserted into the peritoneal cavity of the

bird. Thermocouple insertion was made using either a 22 or 25-gauge syringe needle with a sleeve of polyethylene tubing over the needle shaft. The needle-sleeve combination was inserted through the abdominal wall and into the body cavity of the unanesthetized quail. The needle was then withdrawn, leaving the polyethylene sleeve in the cavity. A thermocouple was inserted through the sleeve and into the peritoneal cavity. The tubing was then removed from the bird and allowed to hang on the thermocouple wire. A drop of collodion (Mallinckrodt Chemical Works, St. Louis, Missouri) applied to the thermocouple at the point of its insertion prevented leakage of body fluids. The thermocouple wire was attached to the plumage using bonewax (Ethicon, Inc., Somerville, N.J.). The thermocouple was inserted into birds, 14 days of age or older, before the experimental run and removed immediately afterwards. This provided for a constant measure of internal body temperature. The thermocouple was not placed into birds younger than 14 days of age until steady-state values of P_{O_2}, P_{CO_2} and %rh were recorded. The bird was then removed from the chamber and the thermocouple inserted. After securing the thermocouple, the bird was placed back into the chamber. The thermocouple was not attached to the young bird while P_{O_2}, P_{CO_2} and %rh were being recorded because of leakage of body fluids and because injuries to the small bird were more common than for the larger animal. The time required to reach steady-state levels was generally longer

for birds 10 days of age or younger than it was for older birds.

G. Calculations

1. Definition of Symbols

$\dot{V}_{I_{(STPD)}}$ = Air Inflow at Standard Temperature and Pressure (ml/min)

$\dot{V}_{I_{(ATP)}}$ = Air Inflow at Atmospheric Temperature and Pressure (ml/min)

$\dot{V}_{O_2}$ = Rate of Oxygen Consumption (ml/min)

$\dot{V}_{CO_2}$ = Rate of Carbon Dioxide Production (ml/min)

BP = Barometric Pressure (mm Hg)

T_a = Room Temperature (C)

T_b = Body Temperature (C)

T_c = Chamber Temperature (C)

$F_{E_{O_2}}$ = Fraction of Oxygen in Outflow Air

$F_{E_{CO_2}}$ = Fraction of Carbon Dioxide in Outflow Air

$F_{I_{O_2}}$ = Fraction of Oxygen in Inflow Air = 21%

$F_{I_{CO_2}}$ = Fraction of Carbon Dioxide in Inflow Air = 0.00%

R = Respiratory Quotient

$\dot{M}$ = Rate of Water Loss (g/hr)

C = Thermal Conductance (W/g/C)

C_{dry} = Dry Thermal Conductance (W/g/C)

E = Evaporative Heat Transfer (W/g)

M = Metabolic Heat Production (W/g)

R = Thermal Insulation (C•g/W)

P_w = Water Vapor Pressure (mm Hg) = 0mmHg on inflow

ρ = Absolute Humidity (kg/m^3)

ϕ = Relative Humidity

p_{s,T_a} = Saturated Water Vapor Density at T_a (kg/m^3)

BW = Body Weight (g)

2. Rate of Oxygen Consumption and Carbon Dioxide Production

All gas equations were derived from Lambertsen (1974). The calculation of $\dot{V}_{I_{(STPD)}}$ is standard procedure where:

$$\dot{V}_{I_{(STPD)}} = \dot{V}_{I_{(ATP)}} \times \frac{BP - P_w}{760} \times \frac{273}{273 + T_a} \quad (1)$$

All factors in equation (1) were measured during the experiment. Oxygen consumption was calculated by:

$$\dot{V}_{O_2} = (\dot{V}_{I_{(STPD)}} / 1 - F_{E_{O_2}} - F_{E_{CO_2}})(F_{I_{O_2}} - F_{I_{O_2}} F_{E_{CO_2}} - F_{E_{CO_2}}) \quad (2)$$

and carbon dioxide production was derived from:

$$\dot{V}_{CO_2} = (F_{E_{CO_2}})(\dot{V}_{I_{(STPD)}} - \dot{V}_{I_{(STPD)}} F_{I_{O_2}} / 1 - F_{E_{O_2}} - F_{E_{CO_2}}) \quad (3)$$

The respiratory quotient (R) was calculated from the carbon dioxide production and oxygen consumption values as:

$$R = \dot{V}_{CO_2} / \dot{V}_{O_2} \quad (4)$$

3. Evaporative Heat Loss

Calculations for the determination of evaporative heat transfer were derived in part from Calder et al. (1974). Percent relative humidity was read directly from the calibration curve and converted into absolute humidity.

$$\rho = [(\phi)(p_{s,T_a})] / 100 \quad (5)$$

The rate of water loss was then read from:

$$\dot{M} = [(\dot{V}_{I_{(STPD)}} \times \rho)/1000] \times 60 \quad (6)$$

The air inflow rate was equal to air outflow rate at all times. Using a value for latent heat of vaporization (580 cal/g water) and a factor for converting cal/hr to watts (1.163×10^{-3}), evaporative heat transfer (E) was calculated as:

$$E = [(580\dot{M})(1.163 \times 10^{-3})]/BW \quad (7)$$

4. Metabolic Heat Production

The following equation for calculating fowl heat production was derived by Romijn and Lokhorst (1961):

$$T = 3.871\ O_2 + 1.194\ CO_2 - 0.380\ P \quad (8)$$

where,

T = heat production (cal)
O_2= oxygen consumption (ml)
CO_2= carbon dioxide production (ml)
P = urinary nitrogen x 6.25 (mg)

Romijn and Lokhorst (1961) also stated that disregarding urinary nitrogen values would not produce an error greater than .6% in the calculated heat production level. Metabolic heat production was calculated from a modified version of equation (8):

$$M = \frac{[(3.871\ O_2 + 1.194\ CO_2)60]\ 1.163 \times 10^{-3}}{BW} \quad (9)$$

5. Thermal Conductance and Thermal Insulation

The following equations were taken from Calder et al. (1974):

$$C = \frac{M}{T_b - T_a} \quad (10)$$

and,

$$C_{dry} = \frac{M - E}{T_b - T_a} \qquad (11)$$

Sample calculations are presented in Appendix 11.

6. Computer

Calculations were performed by an Digital Computer Model LSI-11 (Digital Equipment Corp., Maynard, Mass.).

V. Thyroid Hormone Analysis

A. Total Circulating Thyroxine (T_4) and Triiodothyronine (T_3)

Plasma T_3 and T_4 levels were determined for adult and immature bobwhite (1, 10, 21, 29, 41 and 64 days of age). Blood samples were collected between 1pm and 5pm from all animals except hatchlings, which were sampled at different times during the hatching process. The sampling time was restricted to a few hours to minimize the variation due to possible circadian fluctuations in hormone levels. A detailed examination was made of plasma thyroid hormone levels in the quail at different stages of hatching. Random samples of embryos and hatchlings were made beginning at 549 hr of incubation and continuing at 8 hr intervals through 605 hr of incubation.

All down and feathers were removed from sampling site. The skin was then cleaned with 70% ethyl alcohol and allowed to dry. A small incision was made through the skin and a lancet or syringe needle was used to enter the brachial or

jugular vein. Free flowing blood was removed for T_3-T_4 analysis using a heparinized hematocrit tube (Fisher Scientific Corp., Pittsburg, PA). Each tube was sealed on one end with Critoseal Putty (Sherwood Medical, St. Louis, Mo.) and spun in an IEC MB Microhematocrit centrifuge (International Equipment Co., Needham Heights, MA). The plasma portion of the sample was removed from the hematocrit tube and placed in a Micropet pipette (Clay Adams, Parsippany, N.J.). A quantity of plasma needed for T_3 (100ul) or T_4 (10ul) analysis was put in the pipette, which was sealed on both ends with putty. The sample was kept at 4C in a refrigerator, if it was to be used the next day, or frozen, if not used for several days. These storage measures reduced error due to evaporation of water from the plasma sample.

All plasma samples were analyzed for total circulating T_3 and T_4 levels using a radioimmunoassay kit, developed by Meloy Laboratories (Appendix 12). A Gamma Radiation Model 8725 Analyzer/Scaler (Nuclear Chicago, Des Plaines, Ill.) was used to determine the sample gamma radiation level (Appendix 13).

Individual levels of T_3 and T_4 were determined for each bird tested. In addition, the ratio of T_3 to T_4 was calculated for each bird, to estimate the degree of T_4 to T_3 conversion at each age.

B. Thyroxine (T_4) and Triiodothyronine (T_3) Biological Half Lives

The rate at which T_4 and T_3 are used by an animal were determined by measuring the half lives of the hormones. Half life determinations of T_4 and T_3 were made for the adult and immature quail (21 and 42 days of age) using the technique of Etta (1968)(Appendix 14). The procedure involved first injecting a physiological dosage of the hormone, labelled with ^{125}iodide, into a bird which cannot recycle iodide. Any time decrease in ^{125}iodide levels was due to the breakdown and clearance of the hormone from the animal. The biological half life of the labelled hormone was calculated by measuring the levels of ^{125}iodide in the bird's plasma as a function of time. The biological half lives of T_3 and T_4 in quail younger than 21 days of age could not be tested due to their size limitations. Also, no bird was used for both T_3 and T_4 half life tests.

C. Plasma Albumin Levels

Plasma thyroxine and triiodothyronine are weakly bound to avian plasma proteins, compared to T_4 - T_3 protein binding in mammals, due primarily to the lack of thyroxine binding globulin in birds, with albumin as the major binder of plasma T_3 and T_4. An increase in total circulating T_3 and T4 may not indicate a similiar rise in free T_3 or T_4, the active forms of the hormones. High levels of total circulating plasma T_3 and T_4 may be accompanied by a

similiar increase in plasma proteins which bind and inactivate the hormone. Therefore, plasma albumin determinations must follow an analysis of total circulating T_3 and T_4, in order to estimate the amount of active hormone which is present.

Adult and immature bobwhite (1, 14, 21, and 43 days of age) were tested for plasma albumin levels. Free flowing blood was sampled by puncture of brachial or jugular veins and collected in heparinized hematocrit tubes. The tubes were sealed on one end with putty and spun for 5 min in an IEC MB Micro Hematocrit centrifuge to separate plasma and blood cells. The plasma was then removed and analyzed for albumin content, using the Albumin Colorimetric Determination (Appendix 15).

VI. Statistical Analysis

All data are presented as mean values with vertical lines in each graph indicating ± 1 SE, unless otherwise stated. Data presented for analysis of variance were first tested for variance homogeneity using Bartlett's Homogeneity Test (Gill, 1978). Scheffe's Interval and Modified Scheffe's Interval were used for analysis of data with equal and unequal variances, respectively (Gill, 1978). Statistical comparisons of slopes of lines were performed according to Gill (1978). The level of significance for all statistical tests was set at a probability less than or equal to 0.05%.

Results

I. Growth and Physical Development

Body weights were measured in both the adult and immature quail from day 1 to day 64 after hatching (Part II, Materials and Methods) with a minimum sample size of 8 birds for each test date. There is no increase in body weight until 4-5 days after hatching (Figure 2), approximately 1 day after food intake begins in the quail.

There are two significant* growth phases for the growing quail. An early phase begins at day 5 and runs through day 20 after hatching, during which time the quail gains approximately 1.72 g/day. The second phase includes the period from day 21 to 64 after hatching. At this time there is a daily weight gain of approximately 2.85 g/day.

There is a statistically significant increase from the slope of growth phase 1 to growth phase 2. The correlation coefficient for the age-body weight relationship is 0.998 for both growth phases. This extremely high correlation provides justification for using body weight and age interchangably in all graphs.

*A significance level of $p \leq 0.05$ was used for all statistical tests.

Figure 2. Body mass as a function of age. Ordinate: Body mass (g). Abscissa: Age (days). Line equation was fitted by linear regression analysis.

Line 1 = Day 5 to Day 20 after hatching

Line 2 = Day 21 to Day 64 after hatching

Line 1 : Body Mass = -0.8495 + 1.7203 Age

r = 0.998

Line 2 : Body Mass = -23.0153 + 2.8540 Age

r = 0.998

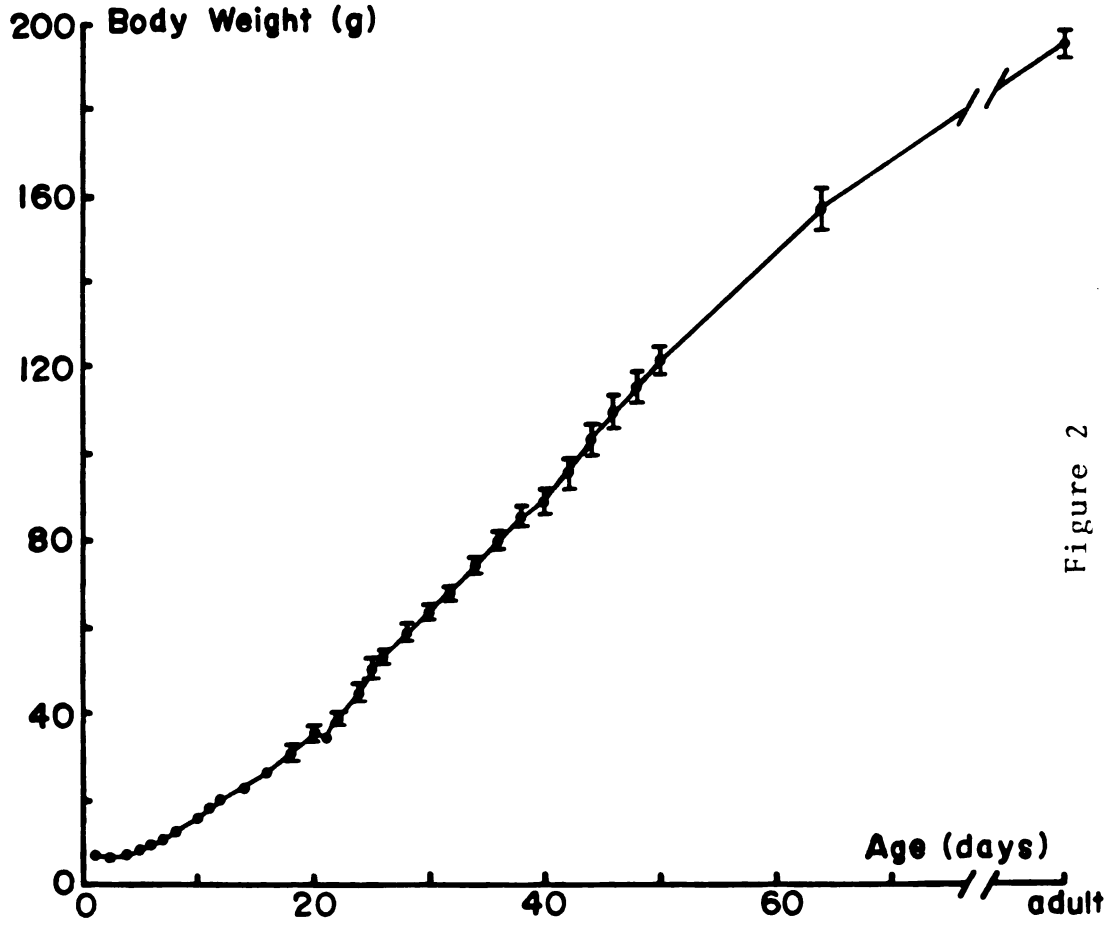


Figure 2

Earlier studies provide information about the growth of wild and captive groups (Stoddard, 1936) and captive quail groups (Lyon, 1962) of bobwhite quail. The body weights from the quail in Stoddard's study were lower on any given test date than the body weights of birds from either Lyon's (1962) or this study. The difference in the growth of wild and captive birds may reflect differences in diet type and food accessibility.

Plumage weights were determined for a minimum of 8 quail at different ages using the technique described in Part III, Materials and Methods. Plumage weight per gram body weight was calculated for each bird tested and expressed in group mean values as a function of age (Figure 3). Weight specific plumage quantity does not increase from day 1 to day 6 after hatching (.Ø2 g/g from day 1 - 6). There is a significant increase in weight specific plumage quantity from the 1, 3, 6 day level to the value at day 1Ø (.Ø413 g/g) and day 14 (.Ø58Ø g/g). This increase suggests that plumage growth is faster than body growth over this period. Plumage quantity decreases significantly from day 14 to day 18. Then body growth shifts to the second phase (Figure 2). From day 18 to day 65, there is a significant increase in weight minus specific plumage quantity. The slope is less than that from day 6 to day 14 and probably results from an increased body growth during phase 2 that is not paralleled by plumage growth. A second significant decrease in weight specific plumage quantity occurs between

Figure 3. Mean plumage/body mass ratio as a function of age. Ordinate: Plumage/body mass (g/g). Abscissa: Age (days). Number above each mean is sample size.

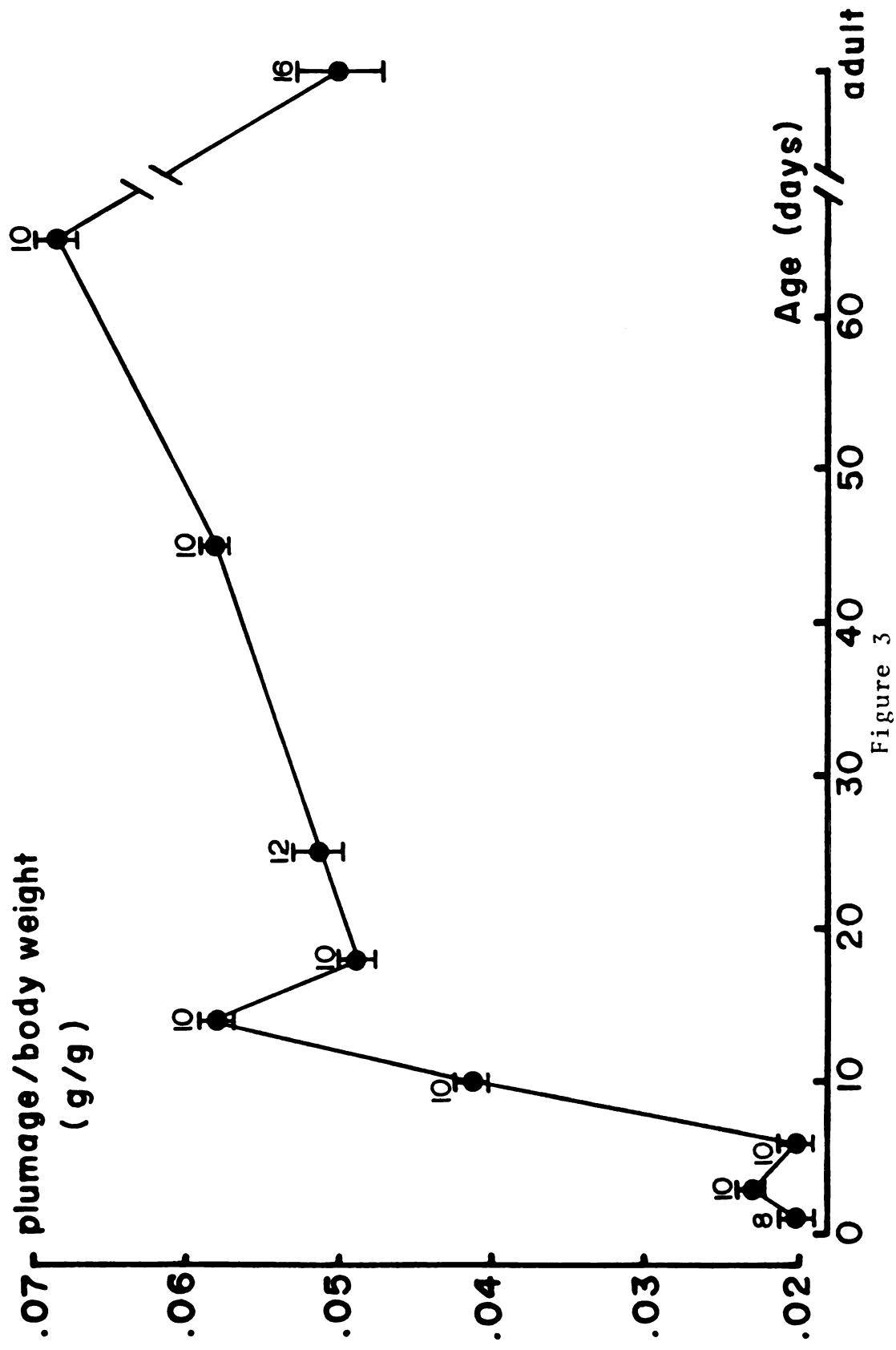

plumage/body weight
(g/g)
.07
.06
.05
.04
.03
.02
0
10
20
30
40
50
60
adult
Age (days)
8
10
10
10
10
12
10
10
16

Figure 3

day 65 and the adult. This is probably due to a reduction in plumage growth with a maintained or increased body growth.

An estimation of skin surface area-to-mass ratio was obtained by using Meeh's (1879) formula (Area = k x $BW^{0.67}$), with Rubner's (1883) bird constant of 10 equal to k. This equation was determined by Drent and Stonehouse (1971) as being a fairly reliable estimation of skin surface area for birds of different size. A second equation (Area = 5.28 x $BW^{0.74}$), derived by Leighton et al. (1966) for use with adult and immature chickens, was also used. Figure 4 shows skin surface area-to-mass ratio as a function of both age and body mass. The largest decrease in the ratio, using either equation, occurs before 20 days after hatching. The large decrease in the ratio before this time could be a major factor in the development of thermoregulation in the young quail.

All data are expressed in weight specific units, rather than surface area values. It is recognized that, in order to access accurately heat transfer values (e.g. thermal conductance, evaporative heat loss), they should be in surface area units (Kleiber, 1970), however, it is currently impossible to determine the "true" functional surface area of a bird. For this reason, it is felt that a precisely measured and widely used unit of expression, such as body mass, is more advantageous than an estimation of surface area.

Figure 4. Estimated surface area-to-mass ratio as a function of age and body mass. Ordinate: area-to-mass ratio (cm^2/g). Abscissa: Age (days); Body mass (g).

Equation A (Meeh, 1879): Area = 10 $mass^{0.67}$

Equation B (Leighton, 1966): Area = 5.3 $mass^{0.74}$

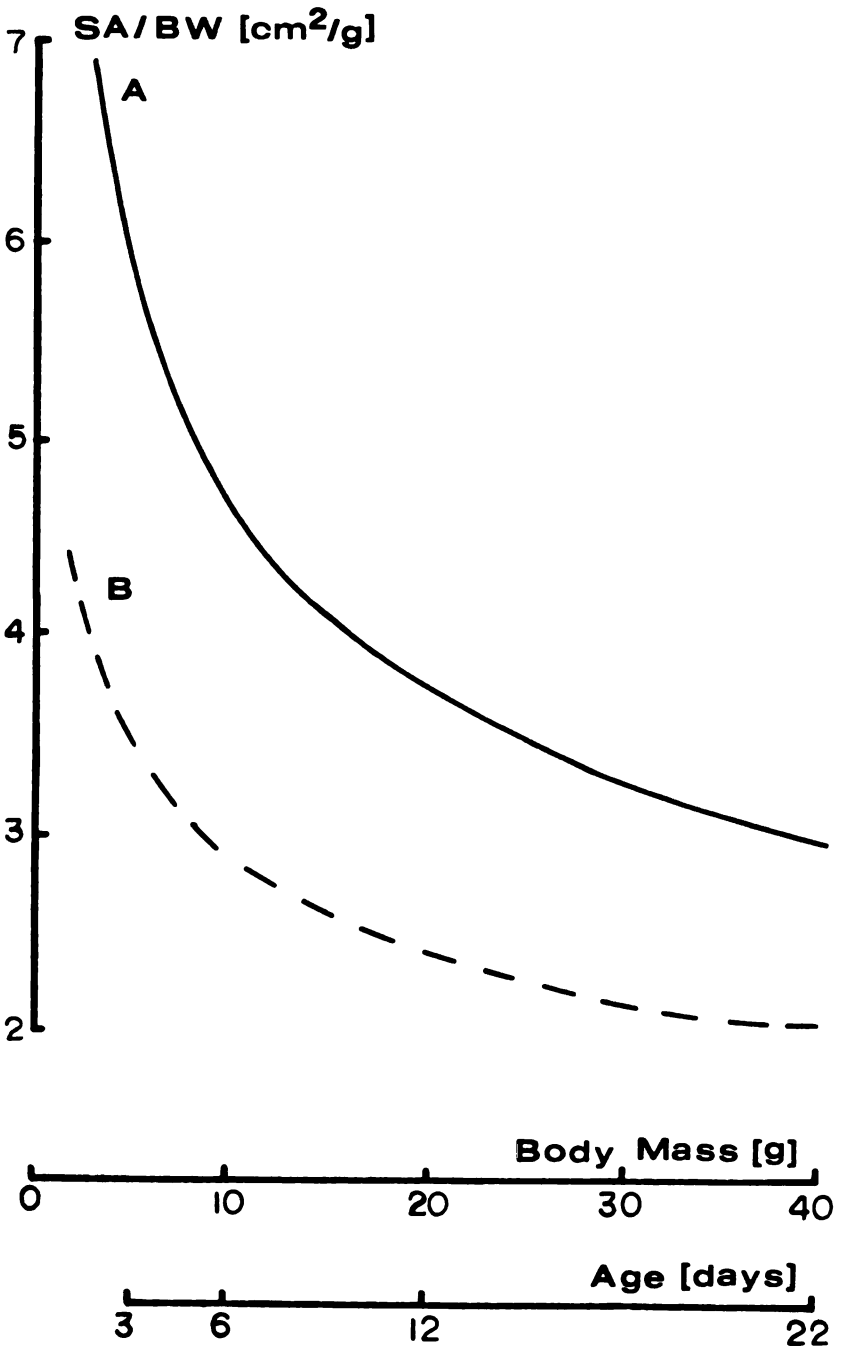


Figure 4

II. Thermoregulatory Ability

Bobwhite were tested at different ages to determine their steady-state thermoregulatory responses to a range of ambient temperatures (T_a). Adult and immature quail (1, 3, 6, 10, 14, 18, 25, 45 and 65 days) were tested at T_a of 10, 15, 20, 25, 30 and 35C. Table 1 shows the sample size (n) for each test group. The shaded area represents that ambient temperature at which quail of a particular age became comatose, with body temperature equal to ambient temperature. Few birds were tested at these temperatures. The experimental groups at days 18 and 25 were divided according to their response.

Prevailing behavior of each test animal was recorded after the run. Table 2 provides a summary of any behavior other than calmness which was observed in at least one bird from a particular test group. Only behavior which was present during the steady-state physiological response is presented. Walking was displayed in the young bird at nearly all T_a. This is presumed to be related to searching for sibling contact and/or a need to increase heat production when cold stressed. Such an active state is assumed to be a "normal" response for a quail of this age to these conditions.

Shivering activity, as assessed visually, is noted as early as 1 day after hatching in the quail, but occurs at different T_a with the development of thermoregulatory

Table 1. Sample sizes of age - temperature groups. Groups below the dashed line are hypothermic and comatose at those exposure temperatures. A = adult.

Temp (C)	Age (days)									
	1	3	6	10	14	18	25	45	65	A
35	8	8	8	8	8	8	9	8	9	9
30	8	9	8	11	8	7	7	9	9	14
25	3	7	8	6	8	9	9	8	10	8
20	0	0	4	3	3	4\6	8	8	4	8
15	0	0	0	0	0	0	4\2	8	8	10
10	0	0	0	0	0	0	0	8	8	8

Table 2. Behavioral responses in age-temperature groups

Age	Ambient Temperature (C) 35	30	25	20	15	10
1*	active	active	active shivers fluffed down	----	----	----
3	active	active	active shivers	----	----	----
6	active	active	active shivers fluffed down and feathers	shivers comatose	----	----
10*	active	active	----	comatose	----	----
14	----	active	active	comatose	----	----
18	----	----	active	active shivers comatose	comatose	----
25	active gular flutter	----	active	shivers	comatose shivers	----
45	gular flutter	----	----	----	----	shivers
65	gular flutter	----	----	----	----	----
adult	gular flutter	gular flutter	----	----	shivers	shivers

Note: active = walking around chamber
* = gular flutter present at 40C
comatose = bird immobile; $T_i = T_a$
---- = no observation

ability. The quail at this age is also able to fluff its down in response to a cold temperature (25C) and possibly increase external insulation. The newly hatched quail is also able to gular flutter in response to heat stress and increase evaporative heat loss (Table 2). This thermolytic behavior is not found in the 1 - 10 day old at 35C, but is present at 40C. The adult quail at 40C is incapable of losing heat fast enough to prevent severe hyperthermia and eventual death.

Internal body temperatures (T_b) were recorded at all test T_a. Figure 5 shows T_b as a function of age at different T_a. From day 1 to day 18 after hatching, T_b is extremely labile at T_a of 25, 30 and 35C. In fact, T_b from day 1 to day 45 after hatching increases significantly from T_a 25 to 35C. At 35C, there is no significant difference in T_b at 25 days and the adult. Also, T_b of the 10 day old is not significantly lower than the 25 day old T_b, but T_b of the 1, 3, and 6 day olds are significantly lower than either the 10 or 25 day old T_b. At 30C, T_b of the 1, 3, and 6 day olds are again lower than the 10 day T_b, but now the 10 day old T_b is significantly below the 25 day old level. At 25C, the 1, 3, and 6 day old T_b is below that of the 10 day old and the 14 day old T_b is below the adult value, but by 18 days after hatching there is no difference. No quail 14 days of age and younger could successfully maintain a T_b above T_a when exposed to 20C. At 18 days after hatching, 60% are able to maintain a steady-state T_b above 20C,

Figure 5. Internal body temperature as a function of age at different ambient temperatures. Ordinate: Internal body temperature (T_b; C). Abscissa: Age (days). Dashed lines represent separation of hypothermic and nonhypothermic responses with the percentage of each response indicated.

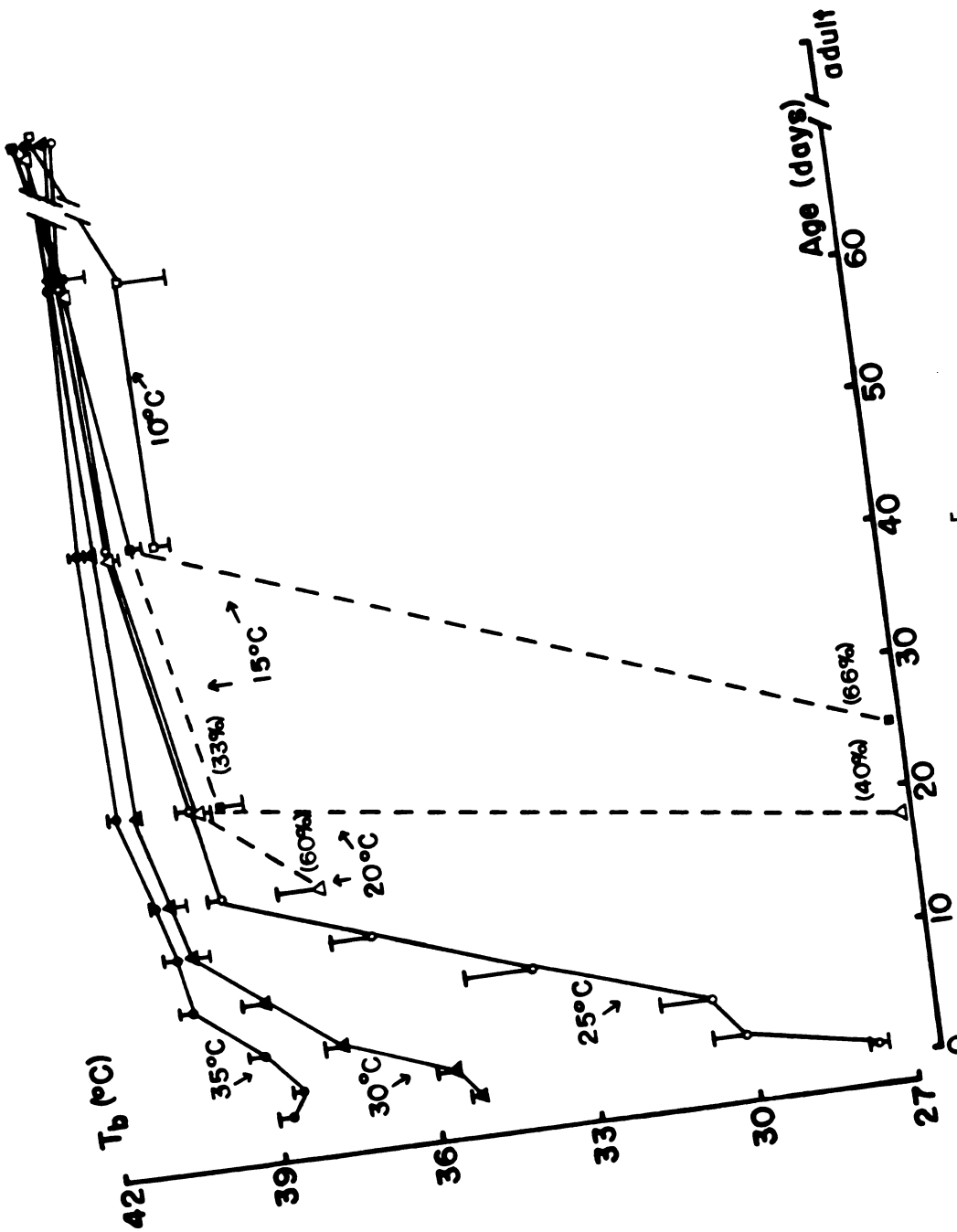

Age (days)
adult
0
10
20
30
40
50
60
T_b (°C)
42
39
36
33
30
27
35°C
30°C
25°C
20°C
15°C
10°C
(33%)
(60%)
(40%)
(66%)

Figure 5

whereas 40% could not. A T_a of 20C is suspected to represent the beginning of a critical survival zone for the 18 day old quail. In Figure 5, the 20C line is dashed at 18 days to accentuate this type of response and divided to show both types of response. The 25 day old T_b at 20C is significantly lower than that of the adult, 65 or 45 day T_b, but there is no difference between the 45 day old and adult T_b response at this exposure temperature. The response of the 25 day old quail to 15C is similiar to that of the 18 day old at 20C, with 33% able to maintain a constant T_b and 66% becoming extremely hypothermic and comatose. At 15C, there is a significant difference between the 45 day old T_b and the T_b level maintained by the 65 day old and adult. A significant difference is also noted between T_b of the 45 day old and adult at 10C, however, all quail, 45 days after hatching and older, maintained a constant T_b when exposed to T_as as low as 10C.

To determine the body to air temperature gradients (T_b-T_a) maintained by young and adult bobwhite quail at different T_a, the difference between T_b and T_a was plotted as a function of age (Figure 6). There is no significant difference in the T_b-T_a interval from 1 to 3 days after hatching, with a significant interval maintained between the 30 and 35C responses starting at 6 days. Through 14 days after hatching, there is no difference in the T_b-T_a interval at 30 and 25C, and only at 18 days does the interval at 25, 30 and 35C begin to plateau at the adult level.

Figure 6. Body-to-air temperature difference as a function of age. Ordinate: Body-to-air temperature difference (T_b-T_a, C). Abscissa: Age (days).

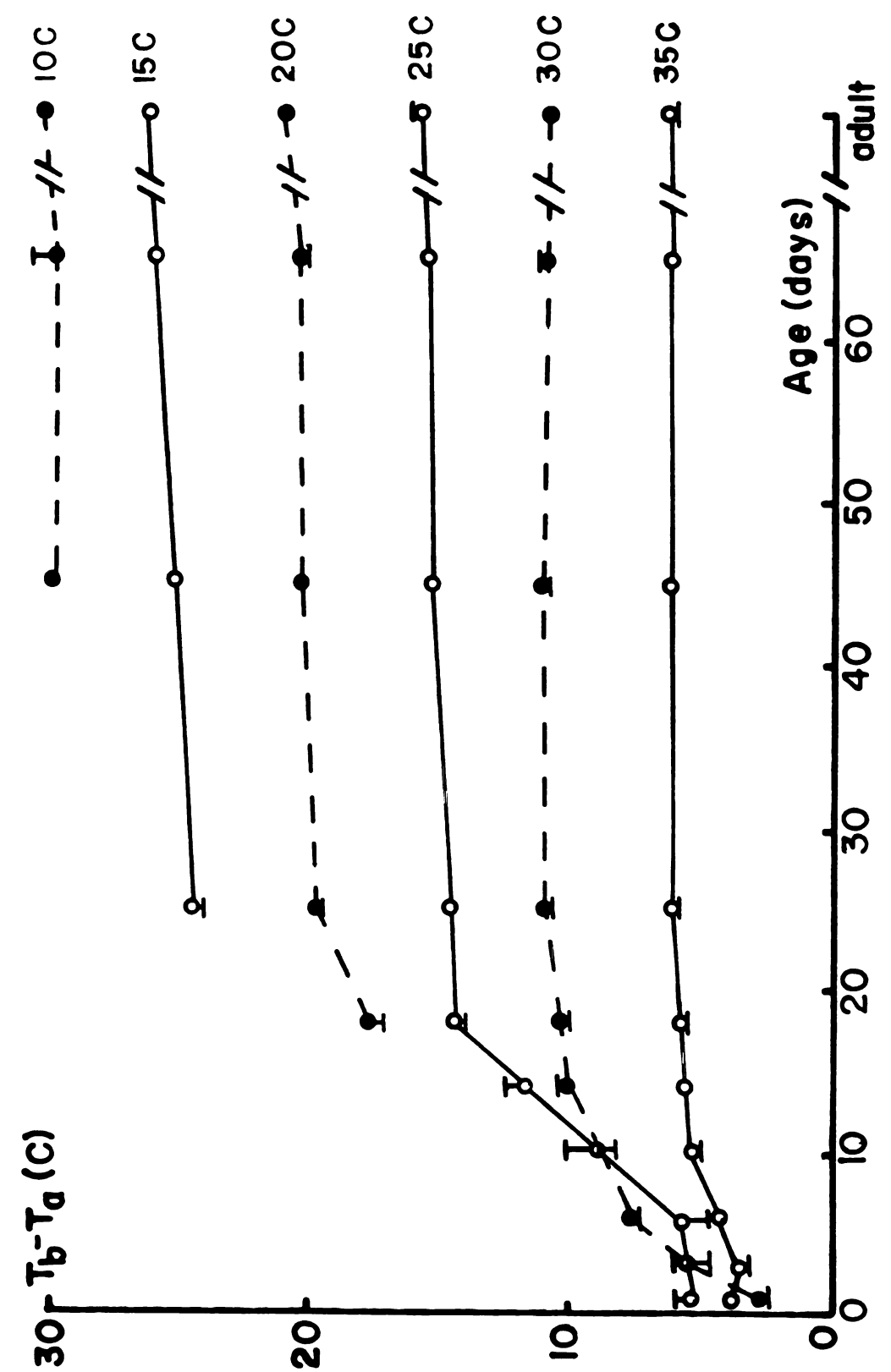


Figure 6

Both the Meeh-Rubner and Leighton equations were initially used to calculate skin surface area and, in turn, to calculate surface area-to-mass ratio. Each group of ratios were plotted as a function of T_b and their slopes were calculated. No significant difference is found between the two slopes, indicating that there is no difference, in the predicted change in surface area as a function of age, between equations. Because the Meeh-Rubner equation is more widely used than the Leighton equation, it was adopted for use in all surface area calculations. To examine the possibility that the surface area-to-mass ratio is related to T_b, a plot is constructed of T_b versus the estimated surface area-to-mass ratio for quail 1-25 days after hatching (Figure 7). This time span encompasses that developmental period when T_b is extremely labile. A significant relationship is found between T_b and surface area-to-mass ratio at 25, 30, and 35C, however, the slopes of the three lines are significantly different from each other. If the three slopes were identical, then it could be suggested that the change in T_b with age is dictated by the surface area-to-mass ratio. Since they are different, it is difficult to determine what the relationship is between T_b and surface area-to-mass ratio.

Metabolic heat production was calculated for each bird using oxygen consumed and carbon dioxide produced, (see Equation 8 of Section G), Materials and Methods. In Figure 8, metabolic heat production (M) is expressed as a function

Figure 7. Internal body temperature as a function of estimated surface area-to-mass ratio. Ordinate: Internal body temperature (T_b; C). Abscissa: Surface area-to-mass ratio (SA/mass; cm^2/g). Line equation fitted by linear regression analysis.

35C : $T_b = 44.136 + ((-0.972)(ratio))$ $r = -.85$

30C : $T_b = 47.860 + ((-2.206)(ratio))$ $r = -.90$

25C : $T_b = 52.220 + ((-4.207)(ratio))$ $r = -.90$

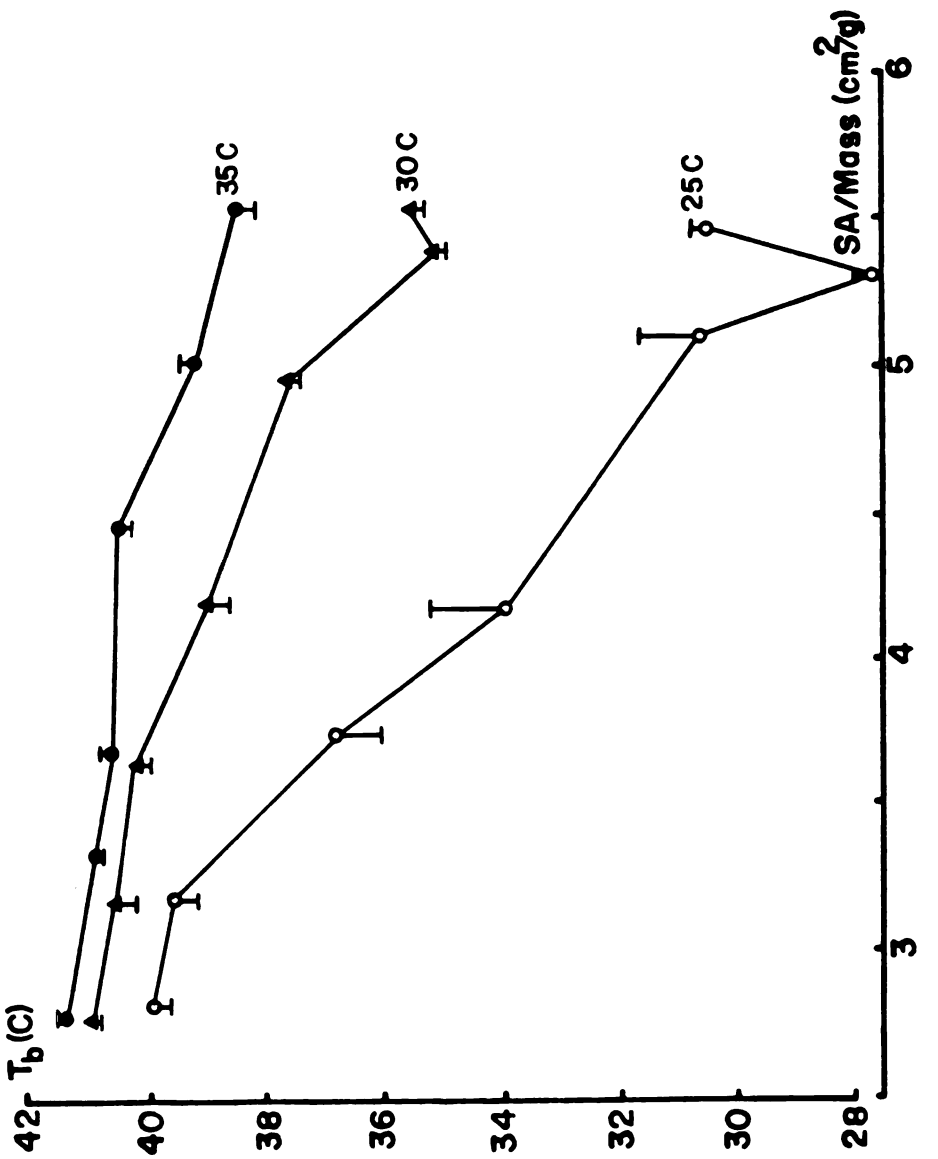


Figure 7

Figure 8. Metabolic heat production as a function of age at different ambient temperatures. Ordinate: Metabolic heat production (M; watt/g x 10^{-2}). Abscissa: Age (days). See Figure 5.

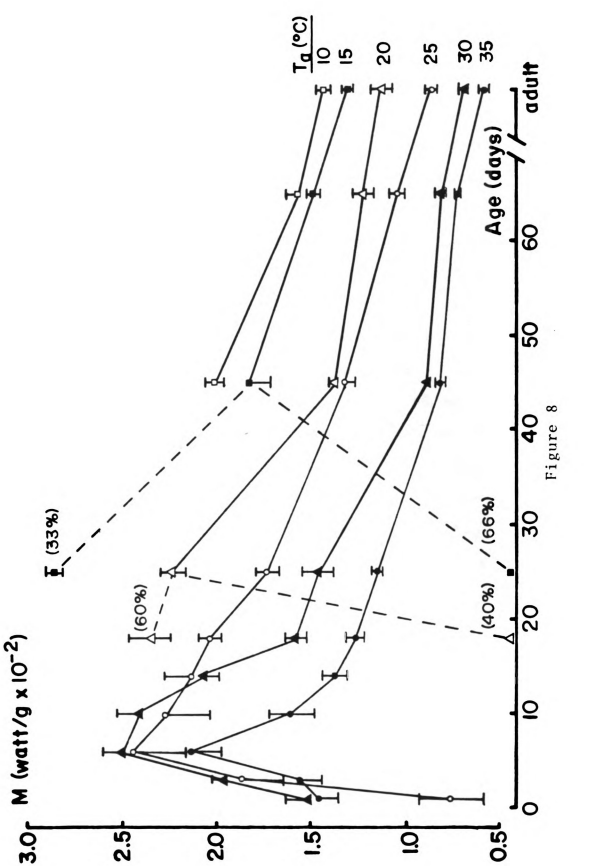

M (watt/g x 10⁻²)
3.0
2.5
2.0
1.5
1.0
0.5
0
10
20
30
40
50
60
Age (days)
adult
(33%)
(60%)
(40%)
(66%)
Tₐ (°C)
10
15
20
25
30
35

Figure 8

of age at different T_a. Metabolic heat production increases significantly from day 1 to day 6 after hatching at 25, 30 and 35C. Metabolic heat production decreases after day 6 to the adult level. The decrease in metabolic heat production from day 6 to day 18 at 25, 30, and 35C is significant. The M at 20C, from day 18 to the adult, is significantly higher than the response of these birds to 25C. There is also a significant difference between the 25 and 30C responses over the same age range, but no difference in M at 30 and 35C. The metabolic responses to 15C at adult, 65, 45 and 25 days of age are significantly higher than those responses at 20C, but the response at 15C is not significantly higher than M at 10C. The metabolic rate of the 45 and 65 day old quails are not significantly higher than the adult at 10 and 20C. The M value at 25 days after hatching is significantly higher than the 45 day old response at both 15 and 20C.

In Figure 9, the M values presented in Figure 8 are plotted as a function of T_a, with each line representing a particular age. The 1 day old quail shows no change in M from 35 to 30C, but did decrease significantly below the 30-35C level at 25C. The M and T_b values indicate that the 1 day old quail at 25C is hypothermic. As seen in Figure 8, M increases with age to day 6. There is no difference in the M response of the 6 or 10 day old between 25 and 35C. In the 10-14 day old quail, there is a slight increase in M from the value at 35C to the 30-25C level. Up to this point, M has plateaued at 30-25C for each age. It is not

Figure 9. Metabolic heat production as a function of ambient temperature at different ages. Ordinate: Metabolic heat production (M; watt/g x 10^{-2}) Abscissa: Ambient temperature (T_a; C). See Figure 5.

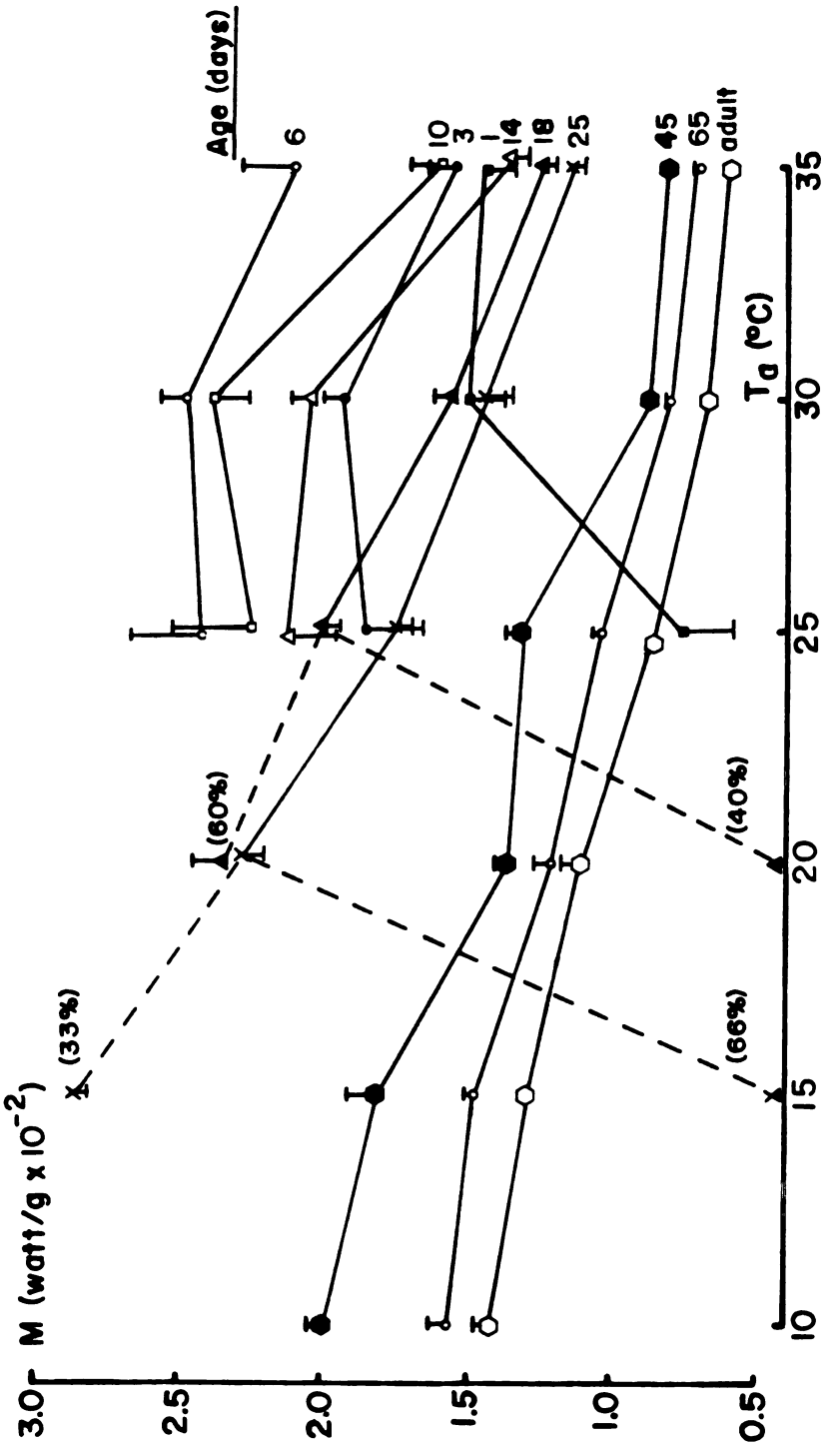

Age (days)
6
10
3
14
18
25
45
65
adult
M (watt/g x 10⁻²)
3.0
2.5
2.0
1.5
1.0
0.5
(33%)
(60%)
(40%)
(66%)
Td (°C)
10
15
20
25
30
35

Figure 9

until 18 days after hatching that a continuous increase in M occurs with a reduction of T_a from 35 to 25C. Metabolic heat production in the 18 day old at 25C is significantly greater than the 35C response and the M at 20C is significantly higher than the response at 30C. The response of the 18 day old at 20C and the 25 day old at 15C is divided because of the heterogenous nature of their response. The maximum M capacity in the 18 day old is not reached at 20C or at 15C for the 25 day old quail. These responses are different from those of the bird 14 days of age and younger, in that they continue to increase heat production up to its lethal T_a, whereas the younger bird displays an M plateau at least 5C before its lethal T_a is reached.

Weight specific M at tested T_a continues to decrease with age after 25 days of age. The M of the 25 day old quail between 20 and 35C is greater than that of the 45 day old over the same temperature range. The 45 and 65 day old quail do not show a significant difference in M at T_a of 15 to 35C, however when both ages are tested separately for statistical differences, they are higher than adult responses. This indicates that even at 65 days after hatching the quail does not function metabolically like an adult.

Respiratory quotient (R) was calculated for the birds at different ages and at the different test temperatures. The increase in R from day 1 to day 6 (Figure 10) is not

Figure 10. Respiratory quotient as a function of age at different ambient temperatures. Ordinate: Respiratory quotient (R). Abscissa: Age (days). See Figure 5.

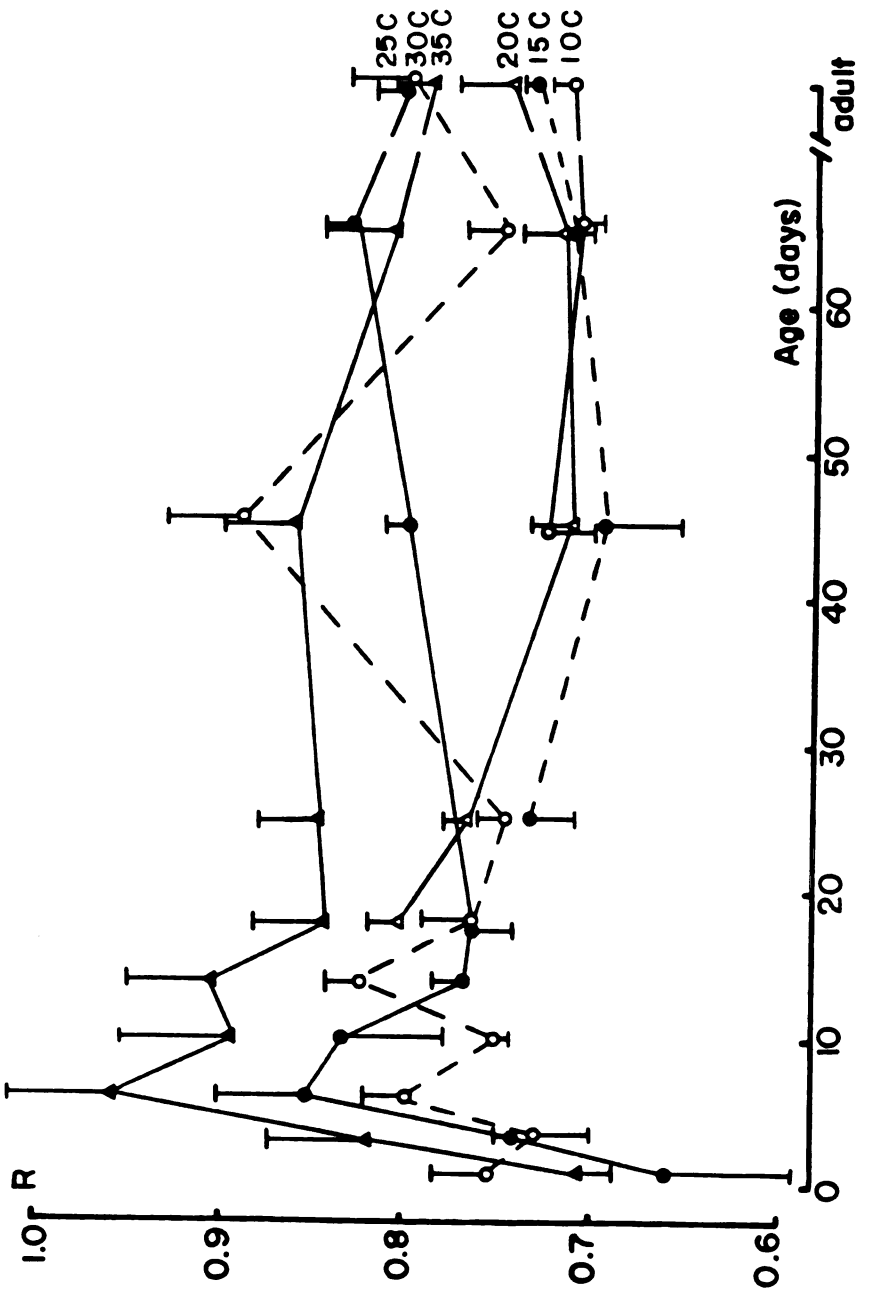

R
1.0
0.9
0.8
0.7
0.6
0
10
20
30
40
50
60
Age (days)
adult
25C
30C
35C
20C
15C
10C

Figure 10

statistically significant, but it suggests that the bird is shifting energy sources from fat to a more carbohydrate-protein source. There is a significant decrease in the R value of the 45, 65 and adult quail from the level at 35, 30 and 25C to that at 20, 15 and 10C. This indicates that the mature bird is metabolizing more fat for energy at low T_a.

The relative humidity of outflow air from the metabolic chamber was measured and used to calculate evaporative heat loss. In Figure 11, evaporative heat loss is expressed as a function of age at different ambient temperatures. Evaporative heat loss in the 1 to 6 day old quail increases significantly from the low level at 25C to the 30C level and to a peak at 35C.

The peak evaporative heat loss at 35C in the 6 day old is significantly greater than the response of the 14 day old to 35C. Also at 35C, the 10 day old evaporative heat loss is greater than the 25 day old response, which is significantly greater than the adult response. When exposed to 25C, there is a significant decrease in the evaporative heat loss from 14 to 25 days after hatching and a decrease in the adult value below the 25 day old evaporative heat loss. The responses at 30C are not different from the 25C from 14 days after hatching to the adult, but the evaporative heat losses at 25C are significantly different from the responses at 35C. From the 45 day old quail to the adult there is no significant difference in the response at

Figure 11. Evaporative heat loss as a function of age at different ambient temperatures. Ordinate: Evaporative heat loss (E; watt/g x 10^{-2}). Abscissa: Age (days).

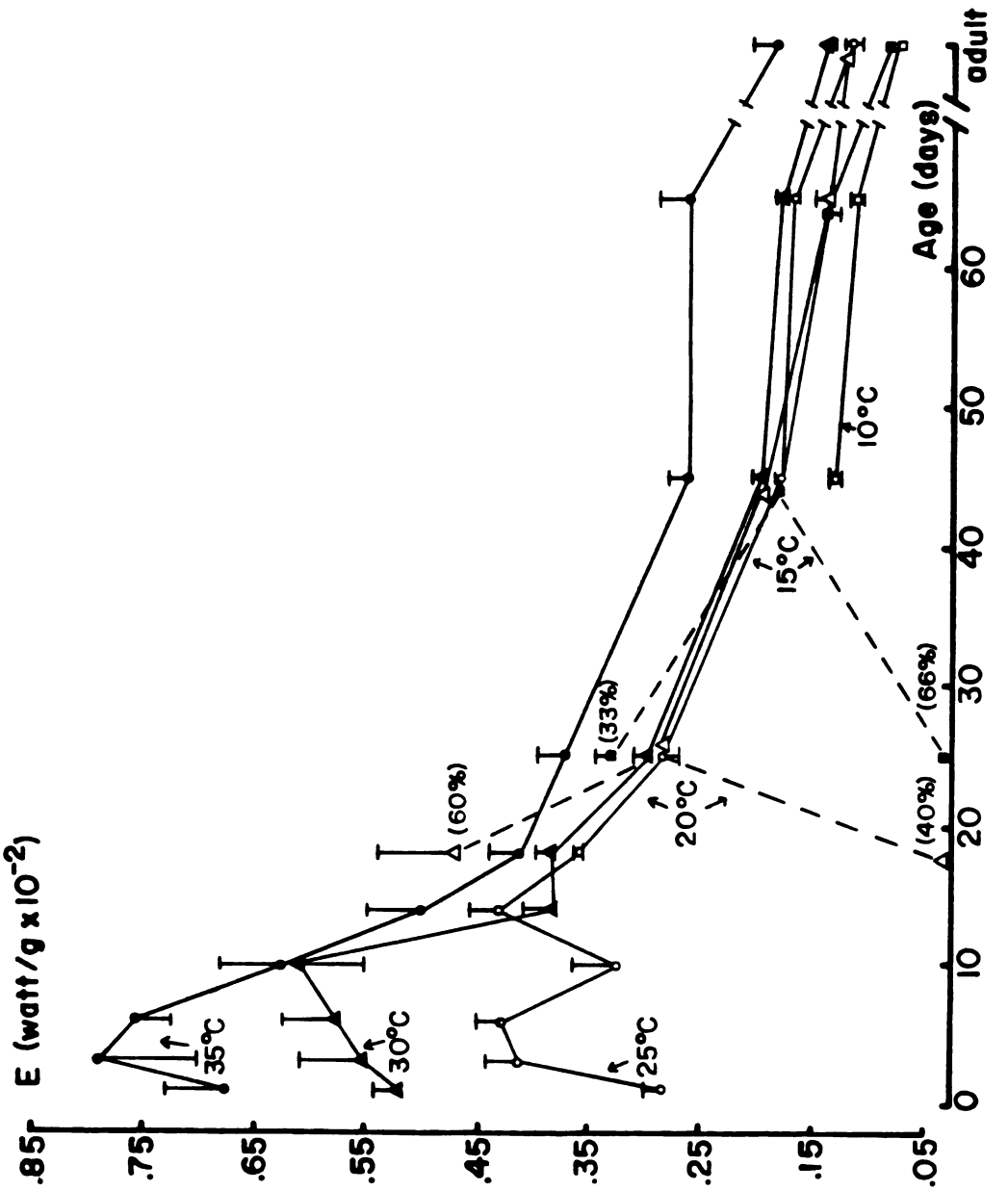

E (watt/g x10⁻²)
.85
.75
.65
.55
.45
.35
.25
.15
.05
0
10
20
30
40
50
60
Age (days)
adult
35°C
30°C
25°C
20°C
15°C
10°C
(60%)
(33%)
(66%)
(40%)

Figure 11

25, 20, 15, and 10C. Also, the 45 day old evaporative heat loss is not significantly different from the adult response at all tested ambient temperatures.

The percentage of the heat loss by evaporation (E/M) is presented as a function of age in Figure 12 . The adult E/M level is reached by 6 days after hatching, although there is no significant difference between ages at any T_a. There is a significant increase in the E/M value at 35C above the 25-30C level at all ages.

Thermal conductance (C), or the inverse of thermal insulation (R), was calculated using Equation 10 (see section G of Materials and Methods). In Figure 13, C is plotted as a function of age. From 1-6 days after hatching, the variance of C is high at any of the three temperatures tested. There is a small increase in C from 1 day after hatching to 6 days, although it is not a significant increase. After day 6, there is a rapid decrease in C at the three T_a over the next 2 1/2 weeks. The C value in the 3 day old quail is significantly greater than that in the 18 day old. Also, the C in the 25 day old and 45 day old at 25C are greater than that in the adult, but there is no difference between the adult and the 65 day old at 25C. At the 30C exposure, there is a significant decrease in C from day 14 to day 18 and between the 25 day old and the adult. There is no significant difference between the response at 45-65 days and the adult response at this temperature. On exposure to 35C, the separate responses at 6 and 3 days

Figure 12. Evaporative heat loss-to-total heat loss ratio as a function of age at different ambient temperatures. Ordinate: Evaporative heat loss-to-total heat loss ratio (E/M). Abscissa: Age (days). See Figure 5.

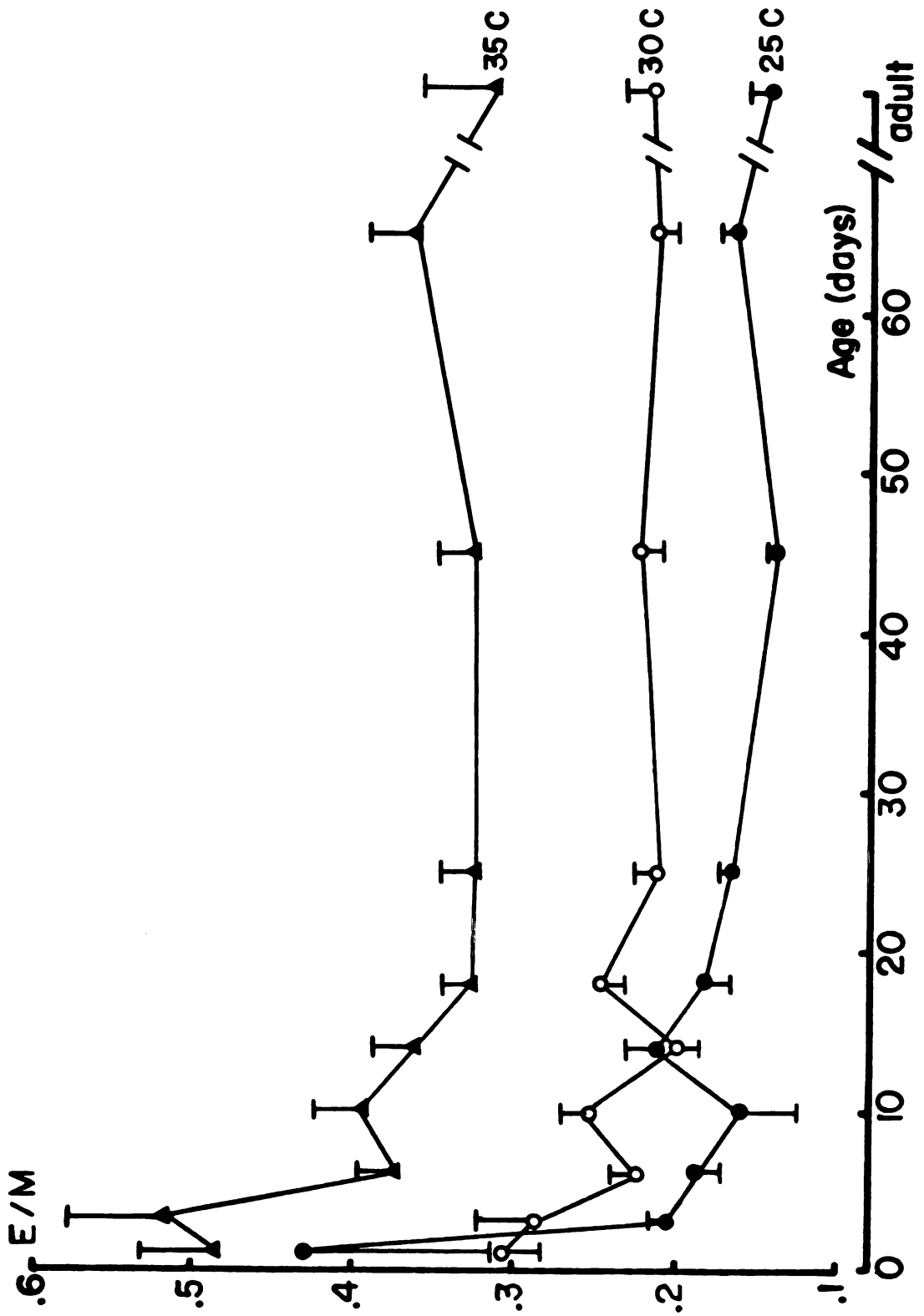


Figure 12

Figure 13. Thermal conductance as a function of age at different ambient temperatures. Ordinate: Thermal conductance (C; watt/g/C x 10^{-2}). Abscissa: Age (days). See Figure 5.

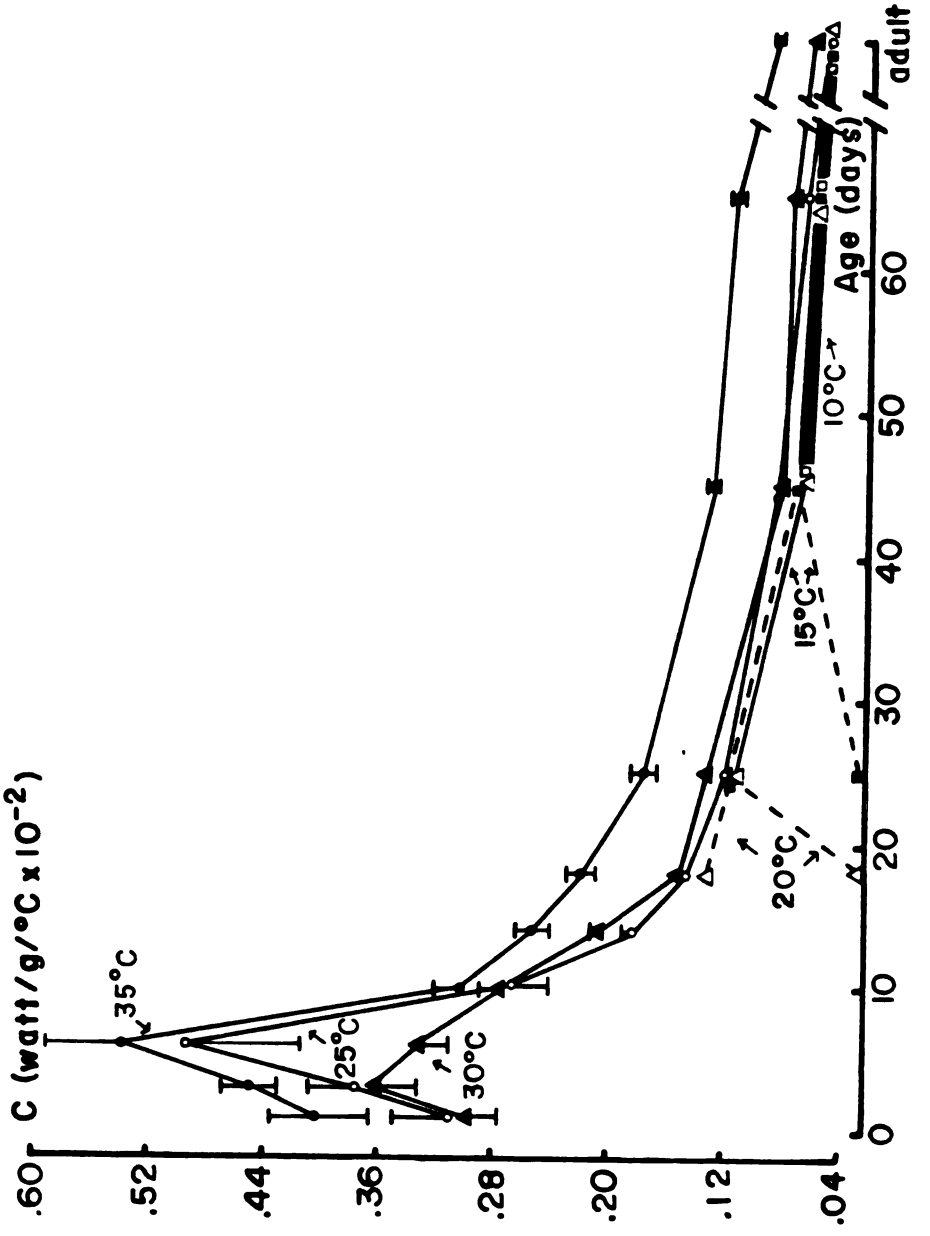

C (watt/g/°C x 10⁻²)
.60
.52
.44
.36
.28
.20
.12
.04
35°C
25°C
30°C
20°C
15°C
10°C
0
10
20
30
40
50
60
Age (days)
adult

Figure 13

after hatching are significantly higher than that of the 18 day old. In addition, the 25, 45 and 65 day old quail have significantly higher thermal conductances at 35C than the adult. It is suggested that even at 65 days after hatching the quail is not thermoregulating like an adult. Thermal conductance values from 14 days after hatching to the adult are higher at 35C than at 30C. This increased C at 35C could be due to increased evaporative heat loss. In order to eliminate this possibility as a source of the increased C, dry thermal conductance (C_{dry}) was calculated.

Dry thermal conductance was calculated for each experimental run using Equation 11 in section G of Materials and Methods. Figure 14 shows C_{dry} as a function of age at different T_a. At 25C, there is still a significant decrease in heat flow 3 to 18 days after hatching and from 25 days to the adult. A significant decrease in C_{dry} occurs from 14 days after hatching to the adult at both 30 and 35C. There is however no significant difference in C_{dry} at 30 and 35C, from 14 days to the adult, showing that the increase in C at 35C (Figure 13) is due to an increase in E.

The thermal balance of the test animals can be tested by comparing the net heat exchange across conductive and convective pathways (M-E) with the body-to-air temperature difference (T_b-T_a). If these two variables satisfy the "linearity criterion" (Gagge, 1936), then steady-state thermal balance was established during the test. In Figure 15, M-E is plotted as a function of T_b-T_a for birds of

Figure 14. Dry thermal conductance as a function of age at different ambient temperatures. Ordinate: Dry thermal conductance (C_{dry}; watt/g/C x 10^{-2}). Abscissa: Age (days). See Figure 5.

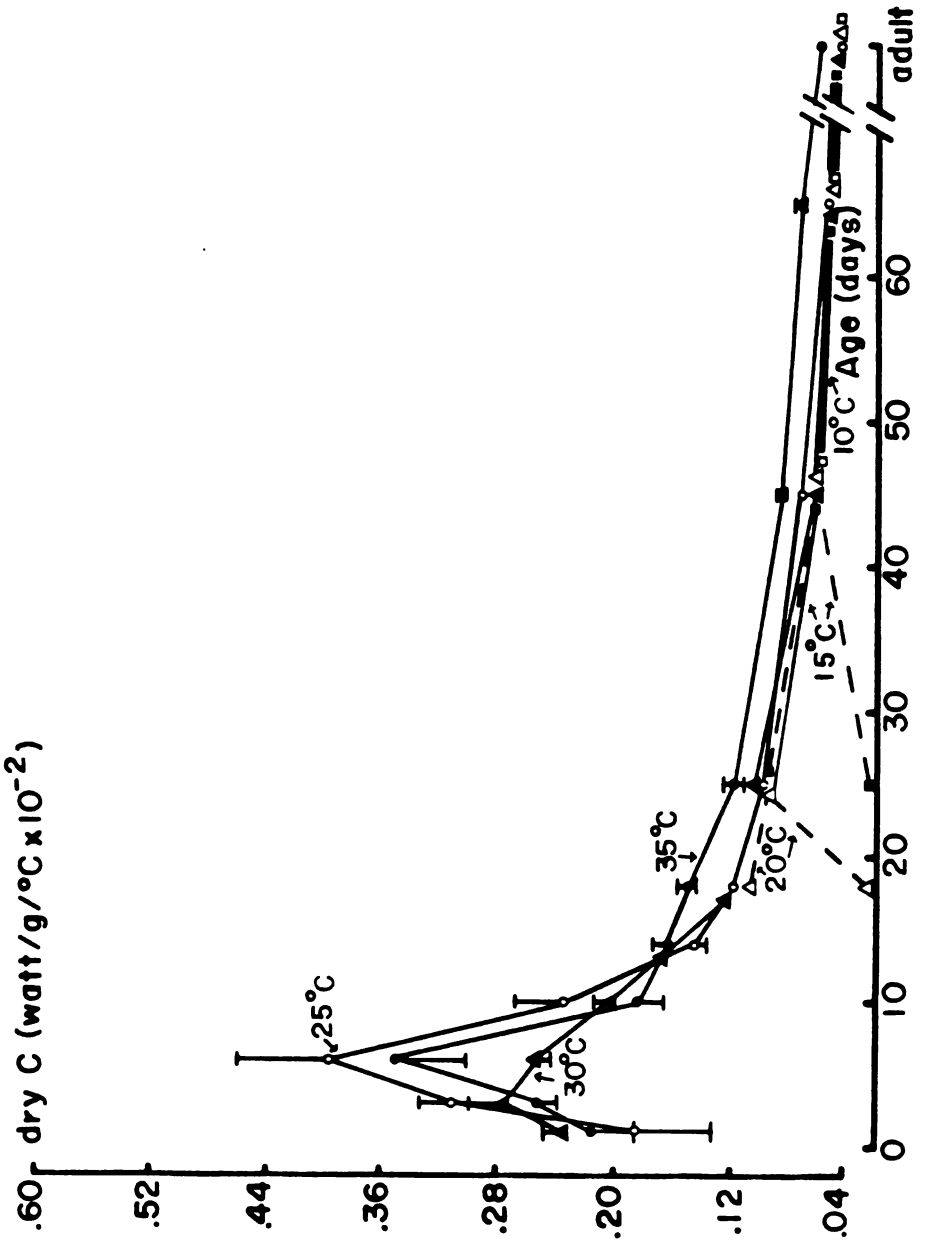

dry C (watt/g/°C x 10⁻²)
.60
.52
.44
.36
.28
.20
.12
.04
0
10
20
30
40
50
60
adult
Age (days)
25°C
30°C
35°C
20°C
15°C
10°C

Figure 14

Figure 15. Metabolic heat production minus evaporative heat loss as a function of body minus air temperature difference at different ages. Ordinate: Metabolic heat production minus evaporative heat loss (M-E; watt/g x 10^{-2}). Abscissa: Body minus air temperature difference (T_b-T_a; C). See Table 3 for linear equations.

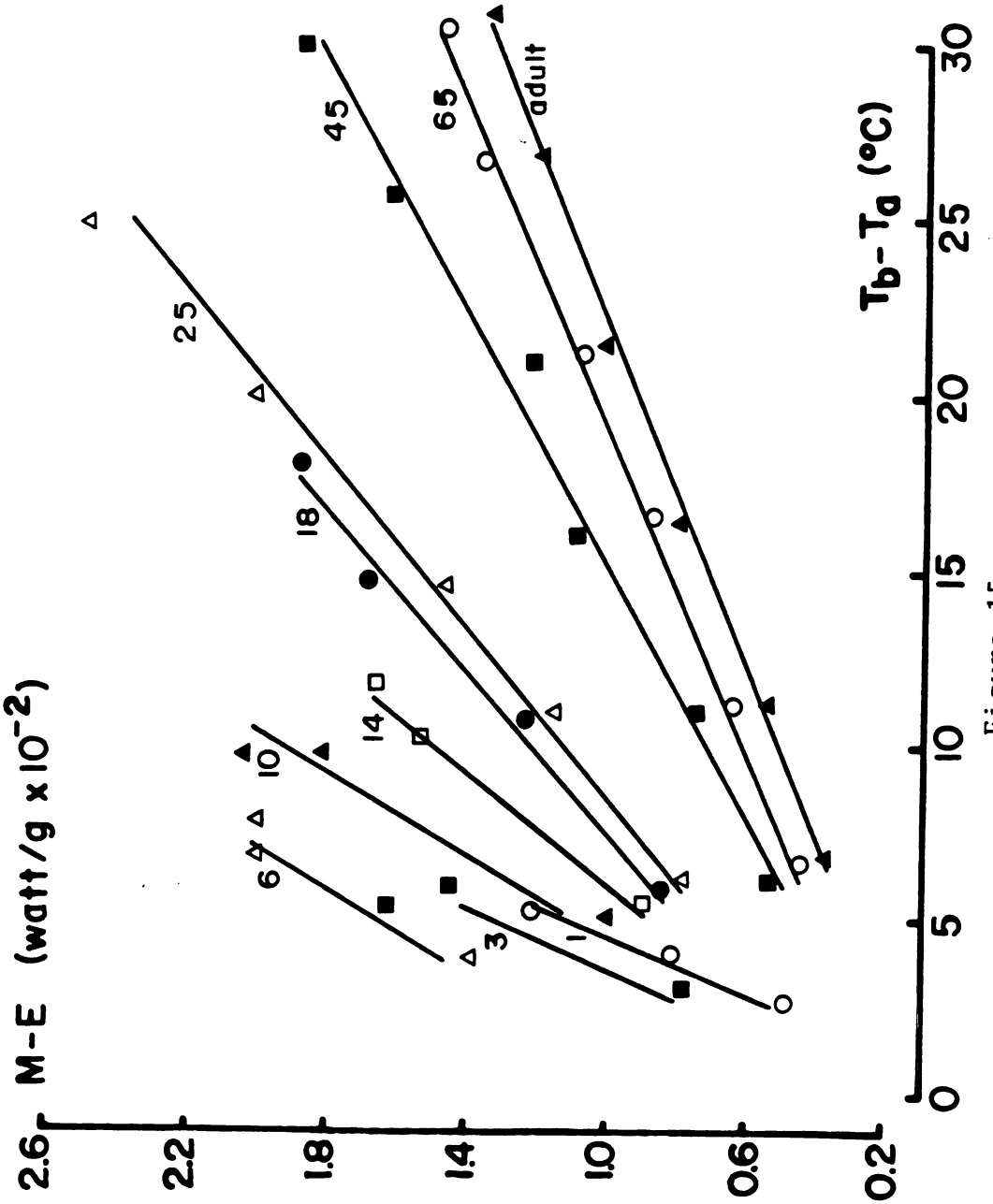

M-E (watt/g x10⁻²)
2.6
2.2
1.8
1.4
1.0
0.6
0.2
0
5
10
15
20
25
30
Tb-Ta (°C)
25
18
14
10
6
4
3
1
45
65
adult

Figure 15

Table 3. Linear regression components of metabolic heat production minus evaporative heat loss versus internal body temperature minus ambient temperature at different ages.

Age (days)	a	b	r	sample size
1	-.1346	.2510 v	.70	19
3	.0359	.2539 v	.78	23
6	.8086	.1674 vw	.68	24
10	.2388	.1689 vw	.73	23
14	.2110	.1290 w	.85	24
18	.3420	.0878 x	.93	30
25	.2041	.0880 x	.94	35
45	.1459	.0566 y	.93	48
65	.1699	.0438 z	.97	48
adult	.0979	.0416 z	.94	55

Note: a = y-intercept

b = slope

r = correlation coefficient

Slopes followed by identical letters are not significantly different.

different ages. The slope of the line in each case represents thermal conductance by convective avenues, with conductive and radiative heat exchange contributing minimally to the slope value. From 10 days after hatching to the adult age, there is a significant decrease in the slope. Table 3 shows the linear characteristics of each line. A linear relationship is found at all ages tested, verifying steady-state thermal balance under these test conditions. There is no significant difference in the slopes from day 1 to day 10 after hatching, however, there is a significant decrease in the slopes from day 3 to day 14. From day 14 to day 18 after hatching, C_{dry} decreases significantly by 32%. Such decreases continue after day 18, but at a slower rate. Dry thermal conductance decreases by 36% from day 25 to day 45 and by 23% over the next 20 days. There is no significant difference between the slope values for the 65 day old and the adult. The relationship of C_{dry} to age is presented in Figure 16. A significant relationship is found between the logarithmic value of the slope of $(M-E)/(T_b-T_a)$ and age.

III. Thyroid Hormone Metabolism

Plasma thyroid hormone levels were measured for the adult and immature quail (1, 10, 21, 29, 41 and 64 days after hatching) in May, 1977 and replicated in December, 1977. No significant differences were found in T_3 and T_4 levels for the two studies. Both sets of data are presented

Figure 16. Slope of metabolic heat production minus evaporative heat loss versus internal body temperature minus ambient temperature as a function of age. Ordinate: b (slope; watt/g/C x 10^{-2}). Abscissa: Age (days). Logarithmic curve fitting used to fit line through points.

$b = .2772 + (-.0569)(\ln \text{age})$

$r = .96$

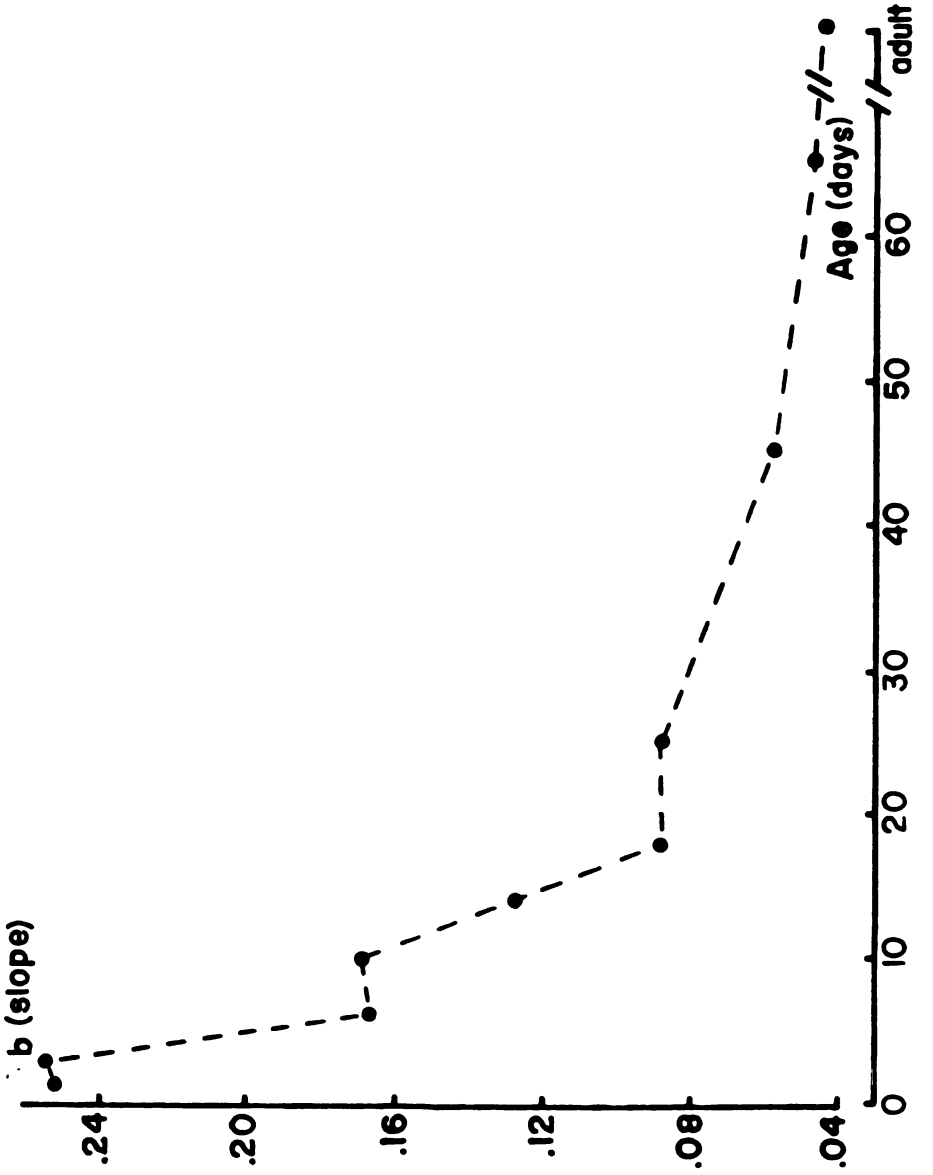


Figure 16

separately in Figures 17, 18, and 19, but statistical analysis was performed on combined data for each age.

Figure 17 shows plasma T_4 levels as a function of age. Plasma T_4 levels are high at hatching and low at 10 days after hatching, however, there was no significant decrease from day 1 to day 10. This is due to the large variance in the thyroid hormone level at hatching, which results from the rapid variations in T_4 at this time. Also, the rise and fall in thyroid hormone levels appear to be unsynchronized with the hatching time or age, as will be demonstrated later. From 10 days after hatching to the adult, there is no significant change in plasma T_4 levels from the 0.5µg% level.

Figure 18 presents plasma T_3 levels as a function of age. There is a insignificant decrease in the plasma T_3 level from day 1 to day 10 after hatching. This change constitutes an average decrease of 74% in plasma T_3 level, but due to the large variance present on day 1, there is no significant difference. Plasma T_3 levels increase significantly from approximately 275 ng% at 21 days after hatching to approximately 550 ng% at 29, 41 and 64 days after hatching. After day 64, the plasma T_3 level decrease significantly from 550 ng% to 300 ng% in the adult (Figure 18).

The ratio of plasma T_3/T_4 is calculated for each test group and is presented in Figure 19 as a function of age. There is no significant difference between grouped data

Figure 17. Plasma thyroxine concentration as a function of age. Ordinate: Plasma thyroxine concentration (T_4; µg%). Abscissa: Age (days). Sample size indicated above or below mean value.

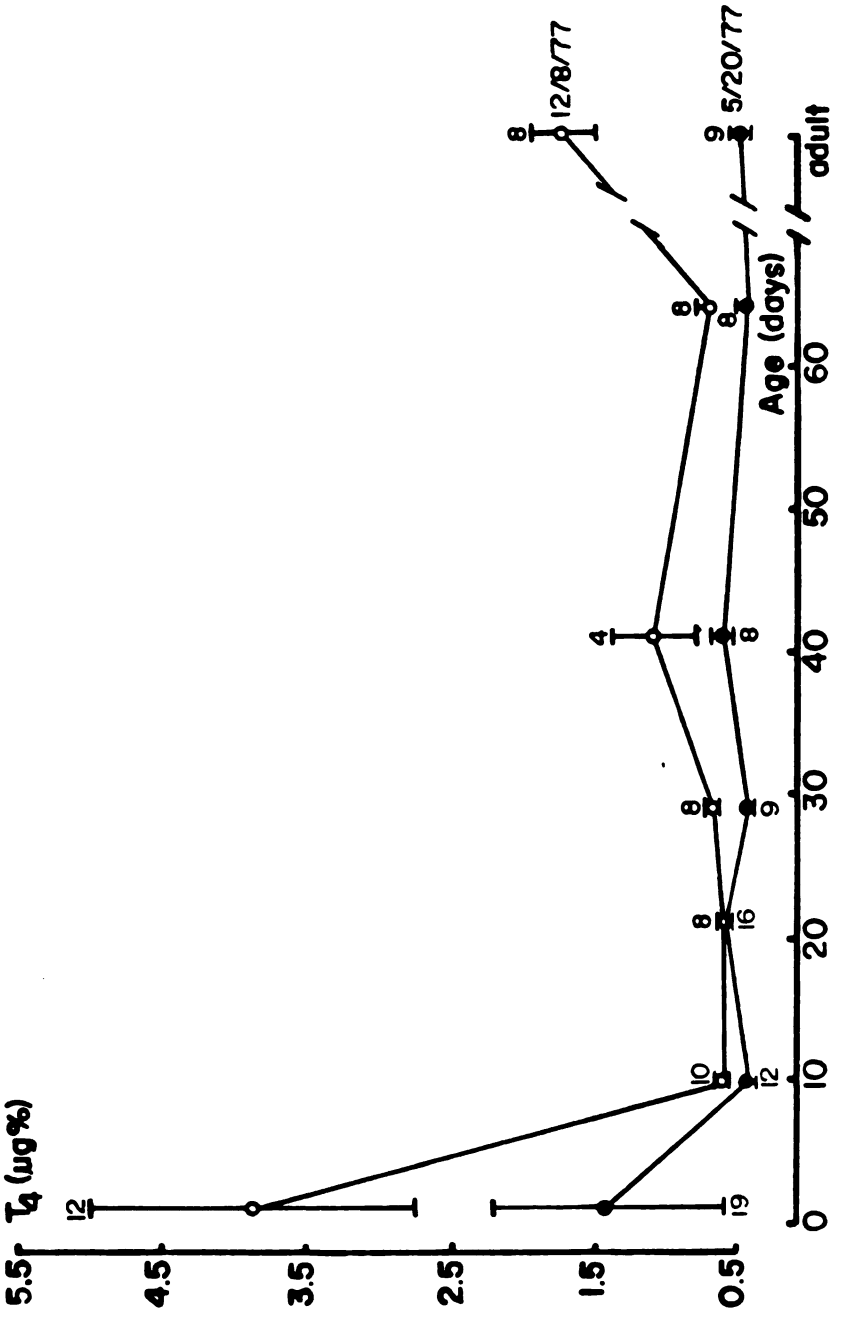

T4 (µg%)
5.5
4.5
3.5
2.5
1.5
0.5
0
10
20
30
40
50
60
Age (days)
adult
12/8/77
5/20/77

Figure 17

Figure 18. Plasma triiodothyronine concentration as a function of age. Ordinate: Plasma triiodothyronine concentration (T_3; ng%). Abscissa: Age (days). Sample size indicated above or below mean value.

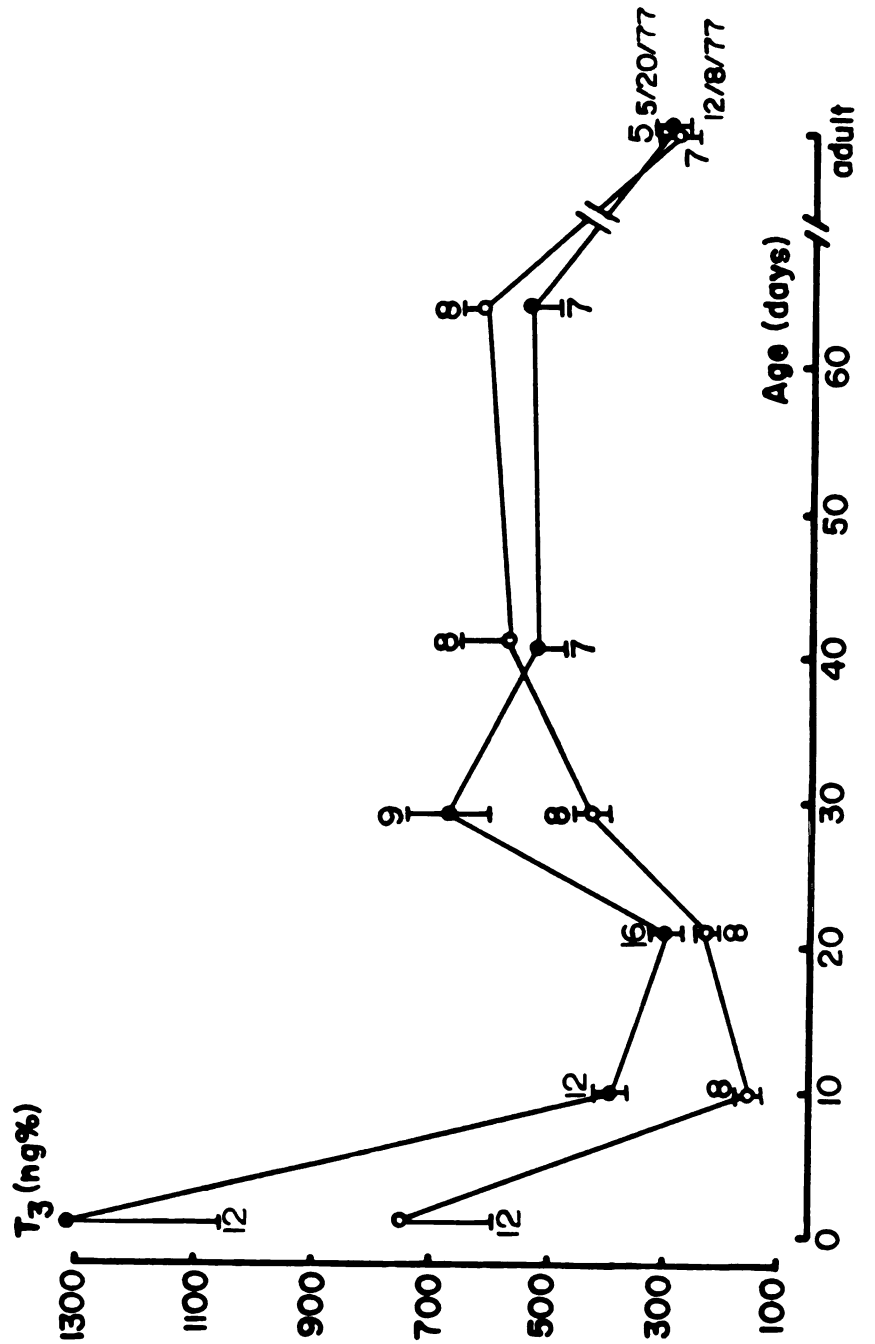

T3 (ng%)
1300
1100
900
700
500
300
100
0
10
20
30
40
50
60
Age (days)
adult
5/20/77
12/8/77

Figure 18

Figure 19. Plasma triiodothyronine/thyroxine ratio as a function of age. Ordinate: Plasma triiodothyronine/thyroxine ratio (T_3/T_4). Abscissa: Age (days). Sample size indicated above or below mean value.

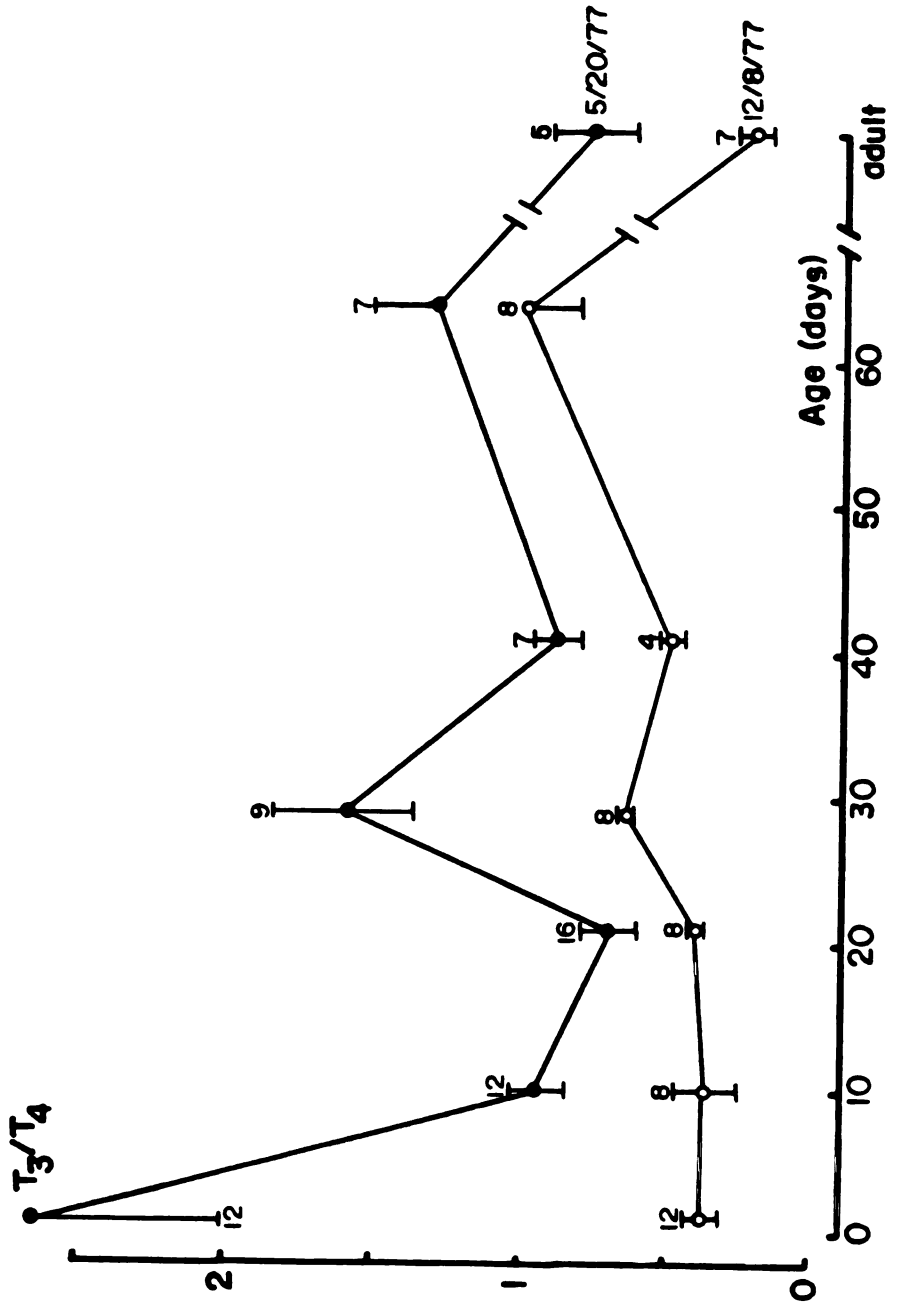


Figure 19

(5/20/77 and 12/8/77) for any particular age, although there is a significant difference between the two runs (5/20/77; 12/8/77). Run 5/20/77 showed no statistically significant differences between any ages, whereas, the 12/8/77 run had a significant increase in the T_3/T_4 ratio from day 10 to day 29 and a significant decrease from the day 29 ratio to the adult.

An analysis of the plasma thyroid levels at hatching was performed to determine when the rise in thyroid hormone levels occurred. Random samples of embryos and/or hatchlings were made from a single group of eggs beginning at 549 hours of incubation and continuing at 8 hour intervals to 605 hours of incubation. Figure 20 shows plasma T_4 levels as a function of age in hours and days. There is no significant difference in plasma T_4 levels at any age tested, although there is a trend toward a peak value at 581 hours of incubation. Figure 21 shows plasma T_3 levels versus age. There is no significant difference between ages, although there is a trend toward a 581 hour peak or when 25% of the quail have hatched.

Biological half-lives were determined for T_3 and T_4 in the adult, 42, and 21 day old quail. Figure 22 shows T_3 and T_4 biological half-lives at the three ages. There is no significant difference between T_3 and T_4 half-lives at the three ages, but there is a significant increase in both hormone half-lives from approximately 3.3 hours at 21 and 42 days after hatching to 5.4 hours in the adult.

Figure 20. Plasma thyroxine concentration during hatching as a function of age. Ordinate: Plasma thyroxine (T_4; µg%). Abscissa: Age (hours; days). Sample size of each age is in parenthesis below mean value. Percentage of total number of birds which had hatched by a particular date is shown above mean value.

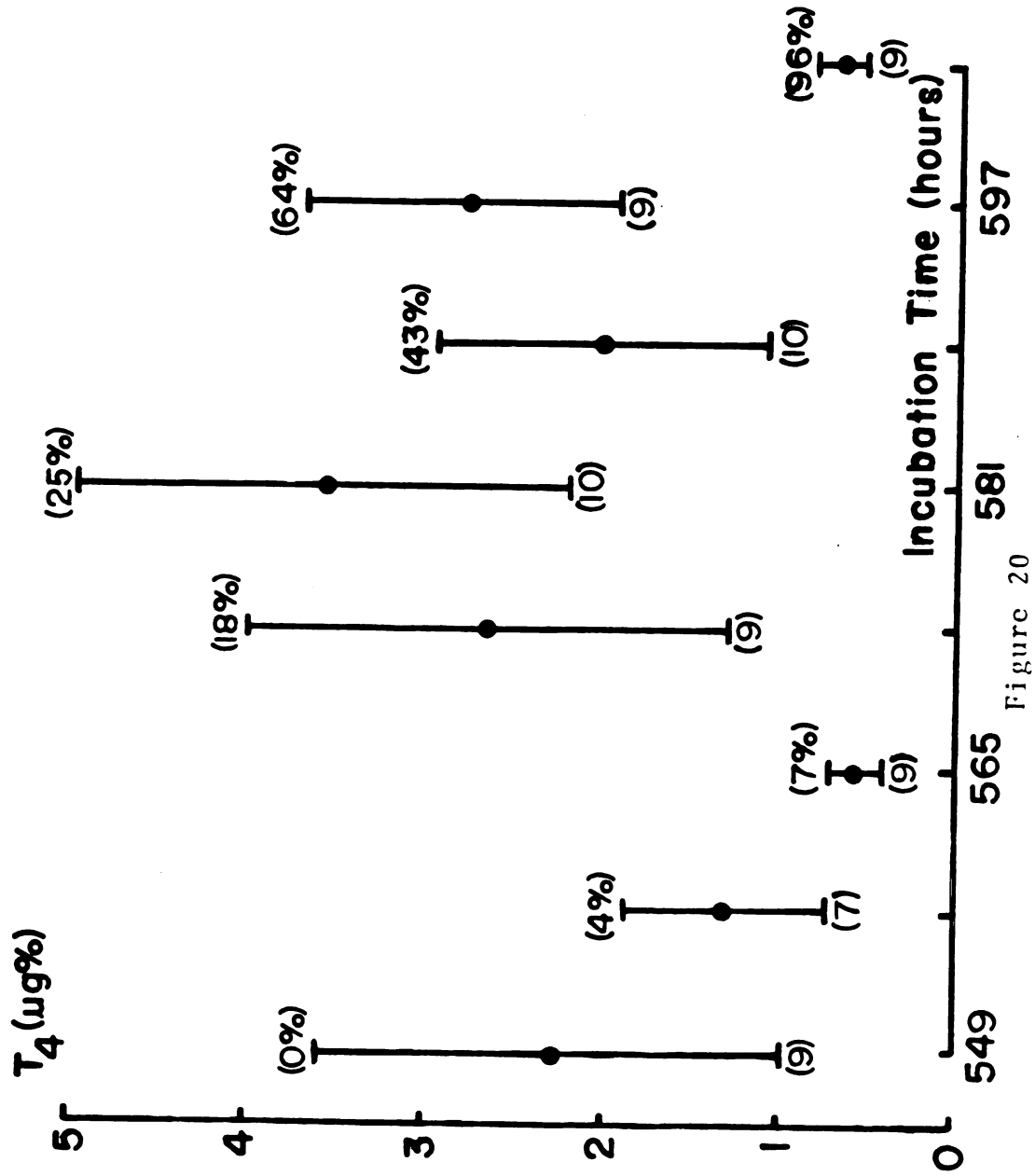

T4 (µg%)
5
4
3
2
1
0
549
565
581
597
Incubation Time (hours)
(0%)
(9)
(4%)
(7)
(7%)
(9)
(18%)
(9)
(25%)
(10)
(43%)
(10)
(64%)
(9)
(96%)
(9)

Figure 20

Figure 20. Plasma thyroxine concentration during hatching as a function of age. Ordinate: Plasma thyroxine (T_4; µg%). Abscissa: Age (hours; days). Sample size of each age is in parenthesis below mean value. Percentage of total number of birds which had hatched by a particular date is shown above mean value.

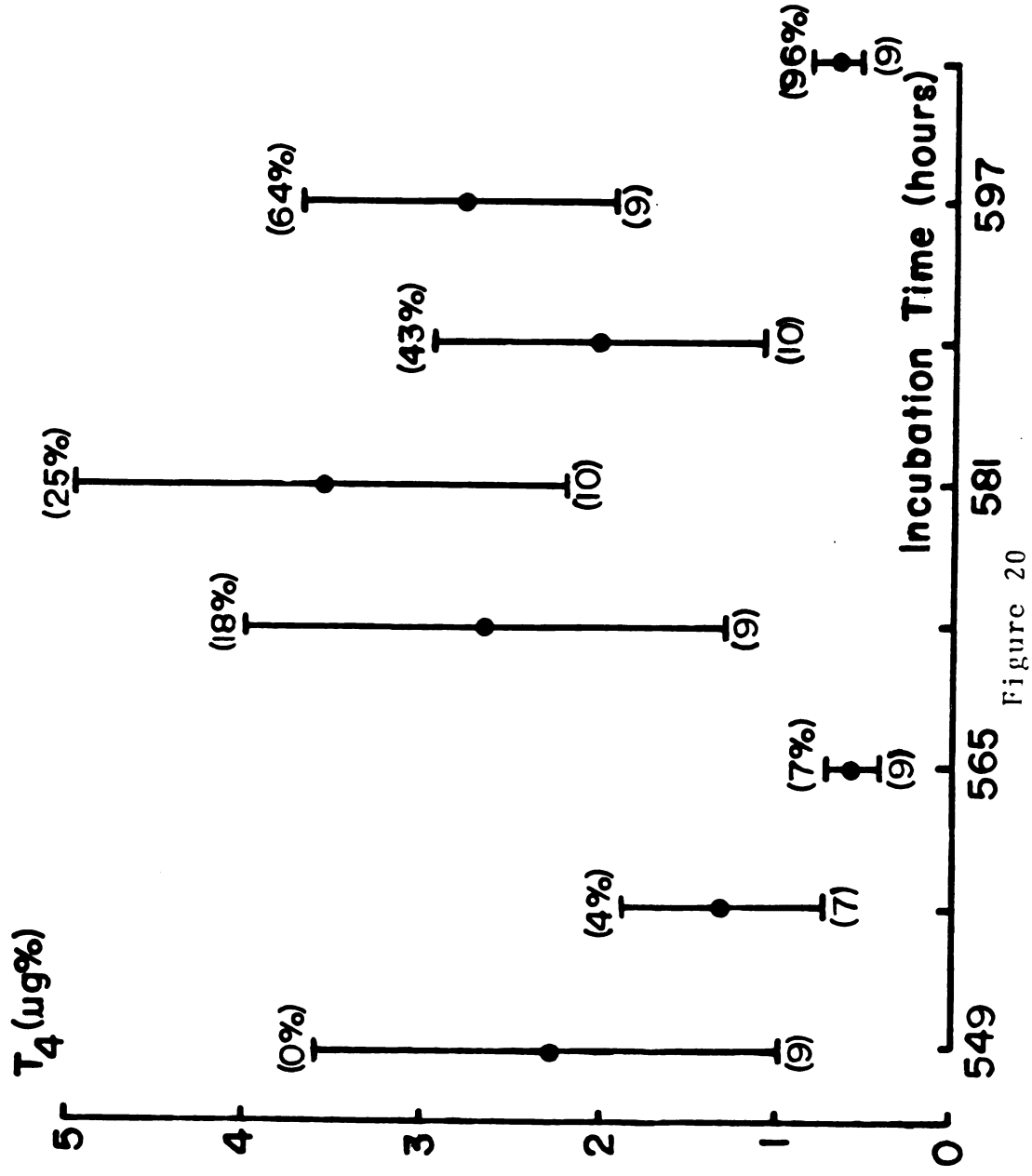

T_4 (µg%)
5
4
3
2
1
0
549
565
581
597
Incubation Time (hours)
(0%)
(9)
(4%)
(7)
(7%)
(9)
(18%)
(9)
(25%)
(10)
(43%)
(10)
(64%)
(9)
(96%)
(9)

Figure 20

Figure 21. Plasma triiodothyronine concentration during hatching as a function of age. Ordinate: Plasma triiodothyronine (T_3; ng%). Abscissa: Age (hours; days). Sample size of each age is in parenthesis below mean value. See Figure 20.

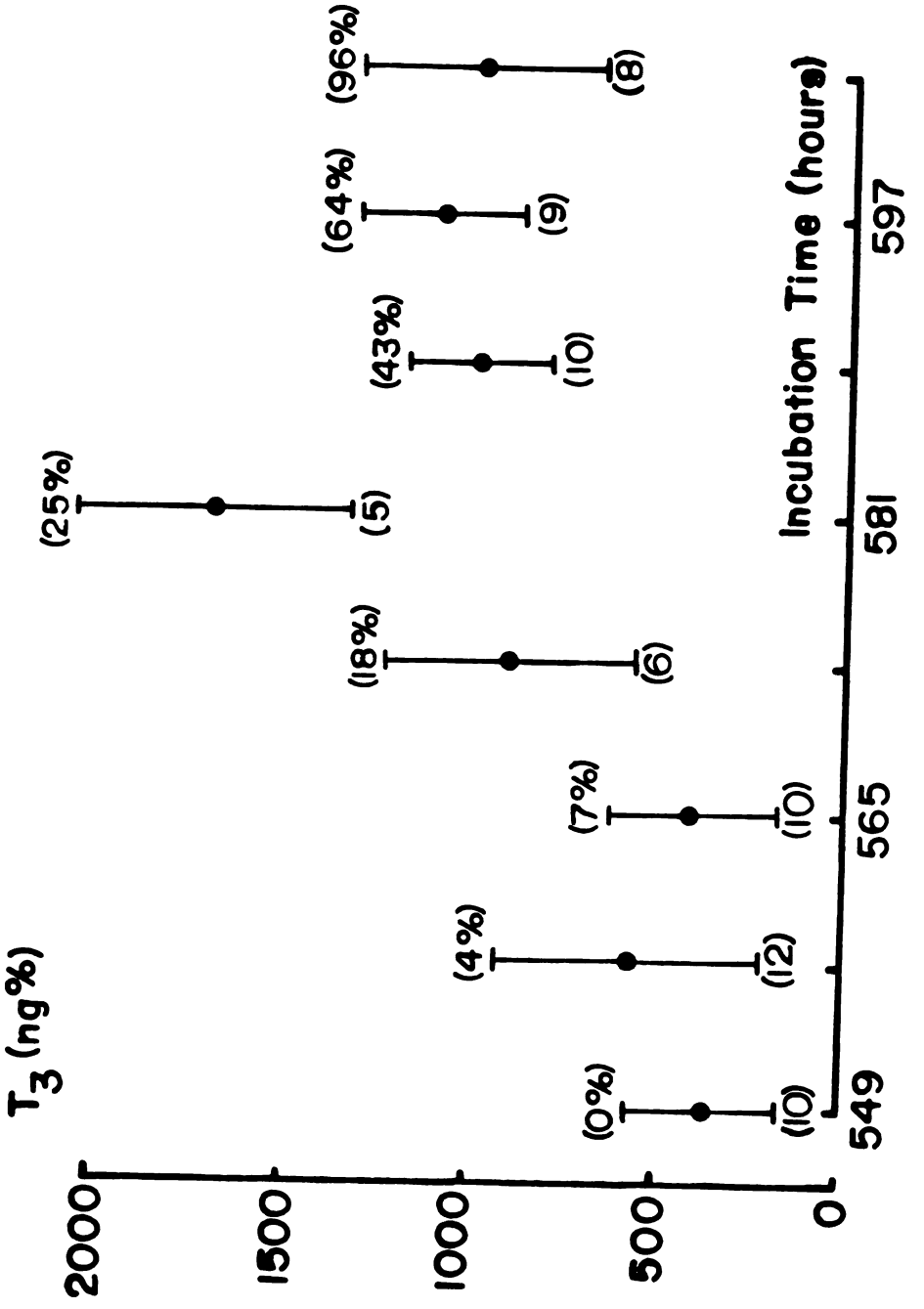

T3 (ng%)
2000
1500
1000
500
0
549
565
581
597
Incubation Time (hours)
(0%)
(10)
(4%)
(12)
(7%)
(10)
(18%)
(6)
(25%)
(5)
(43%)
(10)
(64%)
(9)
(96%)
(8)

Figure 21

Figure 22. Biological half-lives of triiodothyronine (T_3) and thyroxine (T_4) as a function of age. Ordinate: Biological half-lives ($T_{1/2}$; hr). Abscissa: Age (days). Sample size of each age appears in parenthesis above mean value.

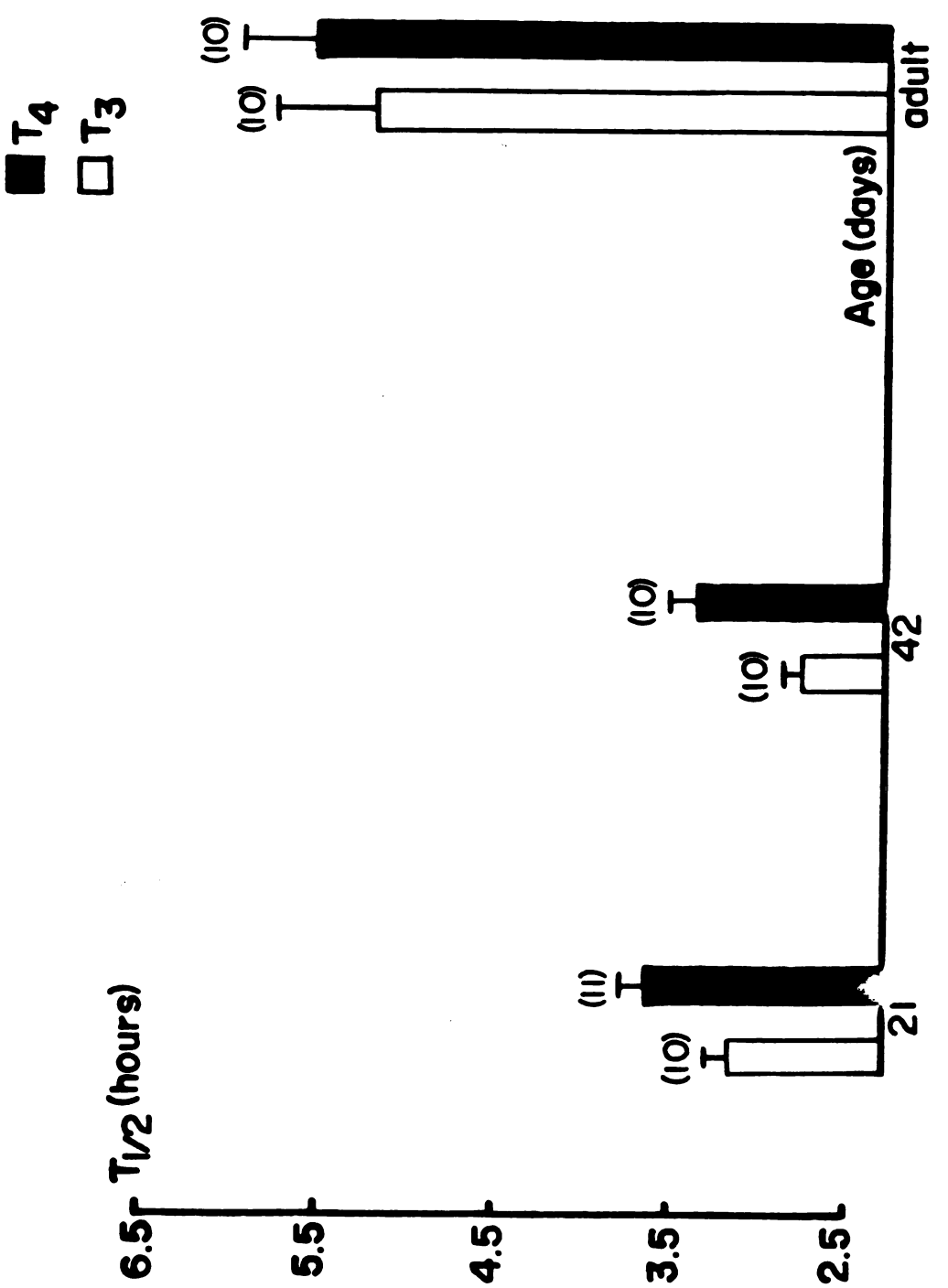

T4
T3
T1/2 (hours)
6.5
5.5
4.5
3.5
2.5
(11)
(10)
(10)
(10)
(10)
(10)
21
42
Age (days)
adult

Figure 22

Plasma albumin levels were measured in the quail from day 1 after hatching to the adult. Figure 23 presents a plot of plasma albumin concentration as a function of age. There is a significant increase in the albumin level from day 1 after hatching to the 21 day old level, and also there is a significant increase from day 14 to day 21 after hatching. Plasma albumin concentration continues to increase significantly from 43 days after hatching to the adult.

Figure 23. Plasma albumin concentration as a function of age. Ordinate: Plasma albumin concentration (g%). Abscissa: Age (days). Sample size of each age appears in parenthesis above mean value.

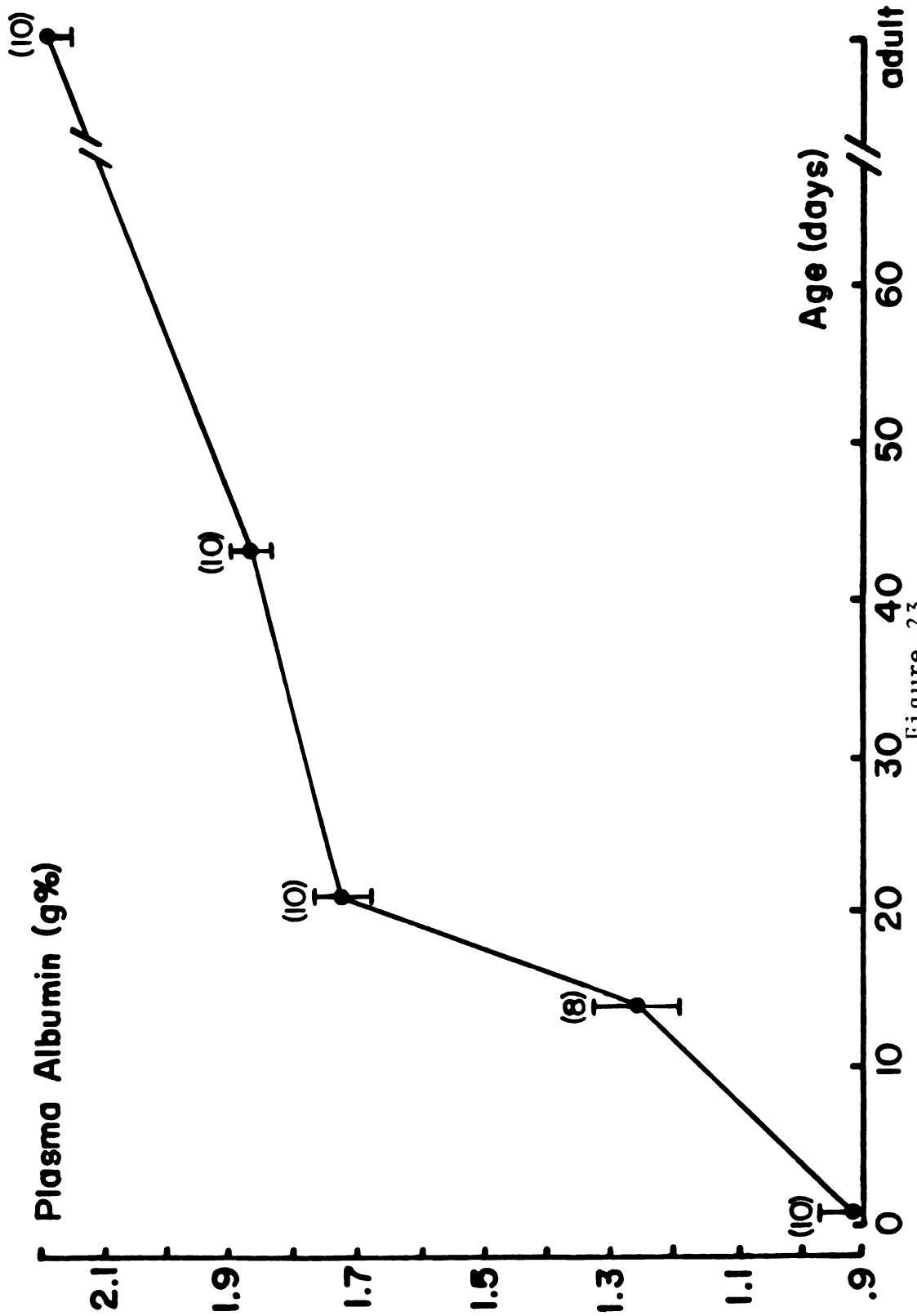

Plasma Albumin (g%)
2.1
1.9
1.7
1.5
1.3
1.1
.9
0
10
20
30
40
50
60
adult
Age (days)
(10)
(10)
(10)
(8)
(10)

Figure 23

Discussion

The ontogeny of thermoregulation is dependent on the development of many factors related to animal growth and function. The growth factors considered in this study are body size, surface area-to-mass ratio and weight-specific amount of plumage. The physiological factors are internal body temperature, metabolic heat production, evaporative heat loss and thermal conductance. Thyroid activity is also considered because it has a major influence on the development of avian thermoregulation (Dawson and Evans, 1960; Singh et al., 1968a; Freeman, 1970; Spiers et al., 1974; Bobek et al., 1977). The thermoregulatory development and growth of the bobwhite can be divided into 3 stages. The stages are day 1 to day 6 (Stage I), day 6 to day 14 (Stage II) and day 14 to the adult (Stage III). There is no distinct age separation of one stage from another, but there are specific characteristics for each.

I. Physical Growth and Development

Homeothermic ability is related to physical characteristics such as body weight, surface area-to-mass ratio and quantity of plumage. Kleiber (1932) indicated that there was a linear, intraspecies relationship between

the log function of body weight and that of metabolic rate. Herried and Kessel (1967) showed that heat transfer coefficients were higher in small birds and mammals than in larger homeotherms due to the reduced thermal insulation and larger surface area-to-mass ratios of smaller animals.

There is no increase in the body mass of the bobwhite until 4 days after hatching (Figure 2), as for other species of hatchlings (Japanese quail - Spiers et al., 1974, Blem, 1978; willow ptarmigan - Aulie, 1976a; painted quail - Bernstein, 1973). This is the result of the young bird's utilization of internal yolk and its limited food intake during the posthatching period (Riddle et al., 1932; Freeman, 1965; Wekstein and Zolman, 1971; Bernstein, 1973; Blem, 1975). After day 4, body mass increases at approximately 1.72 g/day (day 5 - day 20). The growth rate increases after day 20 to 2.85 g/day and continues at this rate through 64 days of age.

There is a significant linear correlation between age and body mass from day 4 to day 20 and day 21 to day 64 after hatching. The relationship of body mass to age, from birth to adult, is a sigmoid function for all animals (Vines and Rees, 1972). Because of the short duration of this study, the plateau portion of the sigmoid curve is lacking from the growth curve. It is expected that continued sampling at later ages would produce the plateau. Other quail species exhibit a growth pattern similiar to the bobwhite. Bernstein (1973) found no increase in the growth

of the painted quail during the first 2 days after hatching. Growth was slow from day 4 to day 9 after hatching and then increased at a faster rate from day 9 to day 35 after hatching. During the latter phase, body mass increased approximately 1.0 g/day and was highly correlated with age. It increases slowly from day 3 to day 9 after hatching, compared to the faster pace after this period. Blem (1978) determined that the Japanese quail gained an average of 2.3 g/day from hatching through 49 days of age.

Blem (1978) found that the total body caloric content of Japanese quail carcasses increased by less than 1 kcal/day from day 1 to day 4 after hatching. Body caloric content increased to a peak value 22-23 days after hatching before decreasing to the 42 day level. Such an increase is generally due to an increase in total lipid content and a decrease in water content (Blem, 1975; Ricklefs, 1967; Dunn, 1975). Blem (1978) also found that the efficiency of energy utilization increased from a low 1-3 day level of 44.8% to an adult level of 64.0% by 2 weeks of age. It is at this time that the peak levels of metabolized and existence energies are reached in the Japanese quail. The bobwhite may experience a similiar change in energy content with age, although the length of the growth period is obviously different between the two species, with the Japanese quail reaching asymptotic weight at 49 days of age and bobwhite not approaching the adult weight until sometime after 65 days of age. The daily weight gain is less in wild bobwhite

(Stoddard, 1936) than in captive quail (Figure 2). This might be due to reduced availability of food and possible metabolic differences.

Surface area-to-mass ratio and thermal insulation are important factors in avian thermoregulation (Dawson and Evans, 1960; Bernstein, 1973; Hudson et al., 1974; Spiers et al., 1974; Dawson et al., 1976). An estimation of an accurate surface area used in the calculation of surface area-to-mass is difficult, if not impossible (Calder, 1972; Kleiber, 1975). One allometric expression of bird skin surface area is:

$$\text{Surface Area} = 10\text{Mass}^{0.667} \qquad (12)$$

This uses Meeh's (1879) standard formula with Rubner's (1883) avian constant of 10, both cited in Walsberg and King (1978) and has been verified for intraspecies application over a wide range of body masses by Drent and Stonehouse (1971). Another expression was derived by Leighton et al. (1966) for the growing domestic chicken, Gallus domesticus. It is:

$$\text{Surface Area} = 5.286\text{Mass}^{0.7446} \qquad (13)$$

The surface area-to-mass ratio of the bobwhite was estimated using the allometric equations of Leighton et al. (1966), and Meeh (1879) and Rubner (1883) to calculate surface area (Figure 4) and then dividing surface area by body mass to obtain the ratio. A large decrease in estimated surface area-to-mass ratio occurs from day 1 to day 14 (Stage I and II) after hatching ,using either

estimate of surface area, and could possibly contribute to a reduction in heat loss over this period.

The bobwhite displays no increase in plumage quantity during the first six days after hatching (Figure 3), with down as the primary plumage cover during this time. Primary and secondary remiges are approximately 1cm long by day 6, with down still attached to the feather tips. From day 6 to day 14, there is a rapid increase in plumage-to-body mass ratio (Figure 3). By day 10, the remiges are unfurling and feathers are starting to emerge along humoral, pectoral and femoral tracts. Primary and secondary remiges are approximately 3.5cm long by day 14 and interscapular, dorsal caudal and dorsopelvic tracts are starting to show feather growth. Stoddard (1936) found that feathers along the wing and scapular regions were long enough at this time to offer the bird some protection from light rains. It is possible that the plumage covering of the 14 day old quail (Stage II) could also provide greater thermal insulation than that found in the younger bird.

From 14 to 18 days after hatching, there is a decrease in the plumage-to-body mass ratio (Figure 3). This is due to body mass increasing at a faster rate than plumage mass (Figure 3). From day 18 to day 65 (Stage III), there is an increase in plumage-to-body mass ratio, but the daily increase is less than that from 6 to 14 days after hatching (Figure 3). This is due to body mass increasing at a slower rate than plumage mass over this period. The Japanese quail

also exhibits rapid plumage growth at an early age, with a 4-fold increase over the first 16 days after hatching (Spiers et al., 1974). In addition, McNabb and McNabb (1977b) found that during this period the insulative capacity of the Japanese quail skin - feather pelts increased 22%. A similiar change is expected in the bobwhite, but over a longer time period. The increased insulative capacity should effectively reduce animal-to-ambient thermal conductance at an early age.

There appears to be little or no change in body size, surface area-to-mass ratio, plumage, and total body caloric content in the quail during the first 4 days after hatching (Stage I). In Stage II, there are large changes in each of these areas which could contribute to the increase in quail thermoregulatory ability. In the next section, the thermoregulatory ability of the bobwhite is examined as a function of age and related to physical growth.

II. Thermoregulatory Development

The areas of thermoregulation which were examined in this study will be presented in order of increasing complexity: internal body temperature, metabolic heat production, evaporative heat loss and thermal conductance. Each area will be examined as it relates to previously discussed material, so that an orderly progression is followed to a final statement concerning the development of thermoregulation in the bobwhite.

The discussion of body temperature (T_b) regulation begins at the age when the quail can maintain a constant, adult level T_b at any of the ambient temperatures (T_a). No change in T_b within the T_a range of 1Ø to 35C (Figure 5) was found for either the adult or 65 day old bobwhite. At 45 days after hatching, there is a significant decrease in T_b below the adult level at 15 and 1ØC. This suggests that the 45 day old quail at 15C is not able to generate heat at a sufficient rate to balance the increased heat loss which possibly occurs at this T_a. The 25 day old is able to maintain a steady-state T_b at a T_a of 2ØC, but at 15C the T_b of 66% of the tested 25 day olds approached T_a. A similiar response was found in the 18 day old at 2ØC (Figure 5). Under these test conditions, T_a of 15C and 2ØC appear to be critical survival temperatures for 25 and 18 day olds, respectively. No bobwhite, 14 days of age or younger (Stage I and II), could maintain a constant T_b above T_a when exposed to 2ØC. The T_b of the 1 to 14 day old quail decreased significantly from its value at 35C to 3ØC and from 3ØC to 25C. From 6 to 14 days after hatching, there are large increases in the weight-specific amount of plumage and decreases in surface area-to-mass ratio. Both changes normally reduce heat loss and could possibly contribute to the increase in T_b which occurs in this time. The physiological factors which might aid in heat production and/or heat loss and affect T_b, will be discussed later.

The quail maintains a relatively constant body-to-air

temperature gradient (T_b-T_a) of 4 to 5C at 25, 30 and 35C (Figure 6) from 1 to 3 days after hatching. A similiar response is found in the 1 to 3 day old painted quail which maintains a T_b approximately 5C above T_a over a temperature range of 19.7C to 40C (Bernstein, 1973). In the 1 to 3 day old bobwhite, there is no increase in body mass, suggesting that surface area-to-mass ratio remains constant. No change in T_b-T_a interval during this time indicates that there is no increase in insulation (Figure 3) with a decrease in T_a and/or an inability to generate heat above the 35C level to increase the T_b-T_a interval. The T_b-T_a interval at these early ages possibly represents the maximum temperature interval that the bird is able to maintain at these ages. There is no change in the interval at 30 and 25C through 14 days of age (Figure 6), suggesting that maximum insulative adjustment and/or maximum heat production is reached at 30C. As the bobwhite matures and increases heat production and conservation mechanisms, the T_b-T_a interval is widened until a plateau is reached at approximately 18 days after hatching (Figure 6).

As indicated earlier, the decrease in surface area-to-mass ratio which accompanies growth, would decrease heat loss from the animal and aid in explaining the increase in Tb (Figure 5) from day 1 to day 25 at 25,30 and 35C. A significant, linear relationship was found between T_b and estimated surface area-to-mass ratio from 1 to 25 days after hatching at 25, 30 and 35C (Figure 7). Assuming that this

approximation provides a valid value for the quail, there is a relationship between the ratio and the development of an adult T_b, suggesting that the decrease in the surface area-to-mass ratio may be contributing to the increase in T_b from day 1 to day 25 after hatching.

A complete understanding of an animal's thermogenic ability and capacity is important in the assessment of its thermoregulatory ability. In the bobwhite, weight specific metabolic heat production changes as a function of age and T_a. It increases in the young quail from a low point at hatching to a peak level 6 days after hatching (Stage I - Figures 8, 9). After day 6, there is a decrease in metabolic heat production to the adult level. A similiar metabolic increase, peak and decline to the adult level has been well documented (Kendeigh, 1939; Dawson and Evans, 1957, 1960; Untergasser and Hayward, 1972; Bernstein, 1973; Hudson et al., 1974; Blem, 1975, 1978). Birds, in general, use yolk material from the absorbed yolk sac during the first few days after hatching (Riddle et al., 1932; Blem, 1975) and rely little on food intake (Bernstein, 1973). During the period (1 to 3 days) when the bird is only using yolk material as an energy source and there is an increase in weight specific metabolic rate, the bird is not gaining weight and may experience weight reduction. Freeman (1965) suggested that the chick during this time is replacing metabolically inactive yolk with actively metabolizing tissue. This increase in active tissue mass produces an

increase in weight-specific metabolic rate and could explain the increase in metabolism from day 1 to day 6 after hatching (Stage I) in the bobwhite.

Other changes in energy metabolism are also occurring shortly after hatching. Once the chick has metabolized all of the stored yolk, it begins to consume food and in this process, changes to a carbohydrate diet. Such a change in energy sources, should produce a change in respiratory quotient (R). In the bobwhite, there was statistically no change in the R value from approximately .7 in the 1 day old to approximately .85 at 6 days after hatching (Figure 10). A possible shift from a high lipid to a carbohydrate diet is indicated. Blem (1975) found a decrease in body caloric content per gram body weight during the time when the bird is using yolk. He attributed this to a decrease in total body lipid content. Once the bird begins to consume food, body caloric content per gram body weight increases as a result of the increased body lipid level (since fat is not a primary energy source at this time) and total body water decreases (Ricklefs, 1967; Blem, 1975; Dunn, 1975). If similiar increases in weight-specific caloric content and energy reserves occurs between 3 and 6 days after hatching in the bobwhite, it might explain the ability of the 6 day old to maintain a steady-state T_b above the 3 day old (Figure 5).

With the shift from a fat to a carbohydrate diet, there are also changes in the young bird's blood carbohydrate

level. Okon (1978) found an increase in Japanese quail liver glycogen and blood glucose levels with the change in diet 5 days after hatching. When the bobwhite begins to consume food (3-4 days after hatching) it changes from a high lipid to a carbohydrate diet (Figure 1Ø). This should provide the bird with a more immediate source of energy for aerobic and anaerobic metabolism and allow for the deposition of lipid stores, which are needed during long-term, ambient temperature stress.

Another explanation for the increase in metabolic heat production at 25C from day 1 to day 6 after hatching is an increase in shivering activity. Shivering was observed at 25C in the bobwhite at 1 day of age (Table 2). Similiar responses to cold have been found in the willow grouse and willow ptarmigan on the hatching date (Myhre et al., 1975; Aulie, 1976a) and in other young birds at 3-7 days after hatching (Odum, 1942; Randall, 1943; Breitenbach and Baskett, 1967; Morton and Carey, 1971) and still others at 1-2 weeks after hatching (Goldsmith and Sladen, 1961; Hudson et al., 1974).

Although shivering activity is present from 1 to 6 days after hatching, there may be changes in shivering intensity (frequency and amplitude) over this period which could explain the increase in metabolism. The shivering response increases with an increase in body size in some birds (Bartholomew, 1966; Aulie, 1976a) and this is correlated with the development of homeothermy (Calder and King, 1974).

The growth of pectoral mass constitutes a major factor in thermoregulatory ability. Aulie (1976a) found a 6-fold increase in EMG amplitude from day 1 to day 3 and an increase pectoral muscle mass from 1.8% body mass on day 3 to 11% body mass on day 12.

Shivering activity was not measured in this study and therefore it is not possible to determine if an increase in shivering intensity produced the increase in metabolism from day 1 to day 6. Young quail at 30 and 35C were not observed to be shivering, although there could have been small tremors. The increase in metabolism (Figure 8) from day 1 to day 6 at 30 and 35C is probably not due to an increase in shivering activity.

Nonshivering thermogenesis could also contribute to the increase in heat production seen from day 1 to day 6 after hatching. West (1965) found no evidence for the presence of nonshivering thermogenesis in the adult bird and no one has discovered brown adipose tissue in the young bird (Freeman, 1967; Johnston, 1971). Still, nonshivering thermogenesis may be present in the neonate. The injection of norepinephrine into the chick produces a small increase in oxygen consumption (Freeman, 1966) and propranolol, a B-adrenergic blocker, causes a steady decline in cloacal temperature and oxygen consumption (Wekstein and Zolman, 1968).

It is probable that the major contributor to the increased metabolism is the change in energy metabolism

between day 1 and day 6 (Stage I). The increase in metabolically active tissue and the increase in carbohydrate metabolism are possible reasons for the rise in metabolic heat production over this period.

There is a significant decrease in metabolic heat production, at 25, 30, and 35C, from 6 to 14 days after hatching (Stage II - Figure 8, 9), although there is no difference in the metabolic response at 25 and 30C. Because metabolic heat production is decreasing during this time, it is not responsible for the increase in T_b from day 6 to day 14, but instead, a decrease in surface area-to-mass ratio (Figure 4) and an increase in insulation (Figure 3) are possible explanations. With these changes, there is possibly a reduction in heat flow out of the bird and a concomitant increase in T_b.

There is no significant increase in the metabolic response at 30 and 25C from day 1 to day 14 after hatching (Figure 9). This suggests that the quail must depend on heat conservation mechanisms during this time to maintain a constant T_b or increase the T_b-T_a interval when going from a 30C to a 25C environment. By 18 days of age (Stage III), the bobwhite is able to increase metabolic heat production from 30C to 25C and even to 20C (Figure 9) to aid in maintaining a constant T_b (Figure 5). At 25 days after hatching, some quail are able to maintain a high level of heat production even at 15C (Figure 9). Hart (1967) indicates that metabolic changes are represented by an

upward extension of the metabolism curve to include lower T_a and/or an upward shift in the slope of the metabolism curve below the lower critical temperature. Both indicators of metabolic change are found in 18 and 25 day old quails (Figure 9). During this time there is an increase in the T_b-T_a interval (Figure 6) at 30 and 25C and a plateau at the adult level. There is neither a significant increase in the quantity of external insulation (Figure 3) nor a large reduction in the surface area-to-mass ratio (Figure 4) over this age range (Stage III), but the quail raises heat production to increase the T_b-T_a interval (Figure 6). Evidence is presented later which suggests that an increase in thyroid activity possibly contributes to the increase in metabolic heat production below 25C at 18 and 25 days after hatching.

There appears to be two periods in the development of bobwhite thermoregulation during which metabolic heat production is a major contributor to T_b maintenance (Figures 8, 9). From day 3 to day 6 after hatching (Stage I), there is an increase in metabolic heat production, possibly resulting from the dietary change which occurs during this time. At some time between day 14 and day 18 (Stage III), metabolic heat production begins to progressively increase at T_a below 30C, possibly due to an increase in thyroid activity (Figure 18).

There is a parallel shift downward in the metabolism curves at 25, 30 and 35C (Figure 9) from 18 to 65 days after

hatching (Stage III). Hart (1967) has shown that increases in insulation are represented by either a parallel shift downward in the metabolism curve with no change in slope and/or a decrease in lower critical temperature to a lower temperature. It is suggested that from day 18 to day 65 after hatching there is decreased requirement for heat production, with increases in insulation, to maintain T_b constant at 25, 30, and 35C (Figure 9).

The respiratory quotient (R) decreased significantly in the adult, 45 and 65 day old quail from approximately 0.82 at 25, 30 and 35C to approximately 0.7 at 20, 15 and 10C (Figure 10). This suggests that the 45 day and older adult quail changes from metabolizing carbohydrates to fats as T_a decreases from 25. A similiar increase in the mobilization and use of lipids is found in other birds during cold stress (Freeman, 1967, 1976).

Evaporative heat loss (E) constitutes a major avenue of heat transfer in birds and mammals, especially at high T_a. Birds lack sweat glands (Jenkinson and Blackburn, 1968) and rely on respiratory evaporation and passive water diffusion through the skin for evaporative heat loss. Bernstein (1971, 1973) has shown that a large portion of the young bird's water loss occurs by diffusion through the skin and suggests that it contributes to the young bird's inability to maintain adult body temperature. Evaporative heat loss (E) in the 1 to 10 day old bobwhite is high at 30 and 35C (Figure 11), although the E/M ratio does not change

significantly from day 1 to the adult (Figure 12). Others (Medway and Kare, 1957; Bernstein, 1971, 1973)have found a higher weight-specific water loss in hatchlings than in adults. Bernstein (1971) reported that the quail hatchling lost as much as 70% of its metabolic heat production at 25C by cutaneous evaporation.

The differences in evaporative heat loss between adult and hatchling are attributed to two factors. First, Bernstein (1971) suggested that the water permeability of the young bird's skin is probably higher than the adult skin. McNabb and McNabb (1977b) verified that the water permeability of the hatchling skin was higher than that of the adult.

The second explanation deals with the process of evaporation. As stated by Calder and King (1974), evaporative heat loss is proportional to the evaporative surface area of the animal and the water vapor pressure difference between that surface and the air. Evaporative heat loss is inversely proportional to the distance between the evaporative surface and the air surrounding the plumage, or the boundary layer. In the bird, body temperature and possibly skin temperature change with age. A change in the temperature of the evaporating surface could alter the surface-to-air water vapor pressure gradient as a function of age. There are also large differences between the surface area-to-mass ratios (Figure 4) and the quantity of plumage (Figure 3) at different ages. The large surface

area-to-mass ratio, possibly thin boundary layer and large water vapor pressure gradient surrounding the young bird could contribute to the high E (Figure 11) at this age. From 6 to 14 days after hatching, there is a decrease in E. This might be due to the decrease in the surface area-to-mass ratio (Figure 4) and the increase in the weight-specific amount of plumage (Figure 3) during this time.

Although evaporative heat loss in the young quail is higher than in the adult, the percentage of the total heat generated by the animal that is lost by evaporation (E/M) does not change significantly as a function of age (Figure 12) and only represents approximately 20% of the total heat lost at 25 and 30C. This suggests that evaporative heat loss in the young quail is not a major factor contributing to the bird's inability to maintain an adult T_b at different T_a. This does not agree with the findings of Bernstein (1971, 1973) which indicate that thermoregulatory development in the quail is dependant on a reduction in evaporative heat loss as a function of age.

Bernstein (1971) found that painted quail hatchlings lost 12 and 6 mg H_2O/g/hr by cutaneous and respiratory means, respectively, at 25C and 7 and 4 mg H_2O/g/hr by the same means at 35C. Later, Bernstein (1973) reported that the quail increased evaporative heat loss at 40C. In the bobwhite, E increases significantly from the 1 to 6 day (Stage I) level at 25C to the 30C level and from the 30C

level to the 35C level (Figure 11). This progressive increase in E as a function of T_a is not found in the adult, which only increases E between 30 and 35C. It could be due to an increase in respiratory and cutaneous evaporation as T_a is increased. Schmidt-Nielsen et al. (1970) reported that some birds and mammals use a counter-current heat exchange mechanism in the upper respiratory tract to reduce respiratory evaporative heat loss. Air which enters the animal during inspiration is warmed as it passes along the respiratory tract and serves to cool the nasal passageways. Water condenses along these passageways from the warm, water-saturated air that leaves the lungs during expiration and enables the animal to conserve both heat and water. In the 1 to 6 day old quail, T_b decreases with a decrease in T_a (Figure 5). With the decrease in T_b, there is less warming of the inspired air in the lungs and a reduction in the water saturation vapor pressure of the air. Less water is carried from the lungs during expiration and lost to the environment at low T_a. Also with the reduction in T_b, there is probably a decrease in skin temperature and the skin-to-air water vapor pressure gradient. The decrease in the temperature of the evaporating surface is a possible explanation for the decrease in E from 35 to 25C in the 1 to 6 day old quail. Bernstein (1971) found that respiratory evaporation in the 0 to 3 day old chinese painted quail (comparable to the 1 to 4 day old in this study) increased when T_a was decreased from 35 to 25C. He acknowledged that

the quail were active when tested in the "stockade-type" apparatus used to separate cutaneous and respiratory water loss and it is possible that the increase in respiratory water loss at low T_a was due to experimental artifact. Respiratory and cutaneous water loss were not separated in this study and therefore it is not certain that the increase in evaporative heat loss with an increase in T_a is due to an increase in respiratory evaporation.

There is a significant increase in E from the 30C level to the 35C level beginning at 18 days after hatching and continuing to the adult (Stage III). The increase in E is due to both panting and gular flutter activity. Gular fluttering was noticed at 40C as early as 1 day after hatching (Table 2). Both panting (Howell and Bartholomew, 1962; Breitenbach and Baskett, 1967; Morton and Carey, 1971; Dawson et al., 1972; Hudson et al., 1974; Myhre et al., 1975; O'Conner, 1975) and gular fluttering (Bartholomew, 1953; Hudson et al., 1974) have been observed in young birds. In the 1 to 10 day old bobwhite, gular fluttering does not occur until T_a is equal to 40C, indicating that the upper critical temperature for the quail at this age is higher than for the older bird. Both thermogenic (shivering) and thermolytic (gular fluttering) behaviors are present in the hatchling bobwhite. This does not agree with other findings (Gotie and Knoll, 1973; Dawson et al., 1976) which suggest that heat dissipating mechanisms appear before heat generating mechanisms in the bird.

The thermal conductance value (C) represents the net heat flow which results from all avenues of heat transfer. It is assumed that many of the physical properties which contribute to thermal conductance do not change with age. These include blood viscosity and tissue density, specific heat and thermal conductivity values. The factors which contribute to the change in thermal conductance include surface area-to-mass ratio, peripheral blood flow, plumage quantity and orientation, evaporative heat transfer, conductive exchange, radiant exchange and wind velocity. The first five factors are considered to be the variables, under these test conditions, which are involved in a change in thermal conductance, with the other factors maintained constant or at a reduced level. Thermal conductance was calculated using the equation presented by Herried and Kessel (1967).

$$Q_l = C(T_b - T_a) \qquad (14)$$

where,

Q_l = heat loss (watt x g^{-1})

C = thermal conductance (watt x g^{-1}x C^{-1})

T_b = body temperature (C)

T_a = ambient temperature (C)

There is a nonsignificant increase in thermal conductance from day 1 to day 6 (Stage I). Even though the increase in C is not significant, several explanations are available for this trend. With the increase in C from day 1

to day 6 there is little change in the T_b-T_a interval (Figure 6) and T_b actually increases (Figure 5). An increase in C does not cause T_b to drop because metabolic heat production is increasing over the same time period (Figure 8). In fact, since the amount of plumage does not increase from day 1 to day 6 (Figure 3), an increase in heat production, as a result of dietary changes, could increase T_b and provide a steeper gradient for heat flow. The increased C may not be large enough to prevent a small rise in T_b (Figure 5). Breitenbach and Baskett (1967) found a similiar rise in thermal conductance in the mourning dove, several days after hatching. They attributed such a rise to an increase in peripheral blood flow, accompanying the emergence of feather quills. This could also produce the increased C seen in the 6 day old bobwhite, since feathers are starting to emerge at this time.

A significant decrease in C occurs from day 6 to day 18 after hatching (Stage II-Figure 13). This is possibly due to a decrease in surface area-to-mass ratio (Figure 4) and an increase in external insulation (Figure 3). The decrease in C is not due to a decrease in E, because it is still present when E is subtracted from the total heat loss (Figure 14). Changes in external insulation may be in the form of changes in plumage type, quantity and/or pilomotor control (McFarland and Budgell, 1970). With increased external insulation (Figure 3), there is greater control of heat loss as seen by the reduced variance in C (Figure 13)

and a greater stability of T_b (Figure 5). Increases in metabolic heat production after the establishment of a sufficient insulative covering (Stage III-18, 25 and 45 days) aids in raising T_b (Figure 5) and maintaining it at a constant level at lower T_a than was previously possible. Alexander (1975) suggested that the development of effective insulation must precede increases in metabolism so as to limit increased heat flow and maintain an efficient thermoregulatory system. This sequence of development is seen in the bobwhite, which increases its weight-specific amount of plumage (Figure 3) from day 6 to day 14 before increasing its capacity for metabolic heat production (Figure 9). After 18 days of age, there is a significant reduction in C, due to continued increases in insulation and a reduction in surface area-to-mass ratio.

Thermal conductance also changes with T_a. Thermal conductance at 25C from 1 to 6 days after hatching (Figure 13), is above the 30C level. This increase in heat loss is possible due to disruption of the bird's insulative boundary layer, which accompanies the shivering activity at 25C and is not due to an increase in evaporative heat loss, since C (Figure 13) and dry C (Figure 14) are identical at 25C. There is also a significant increase in C from 30 to 35C in the 1 to 6 day old and the 18 day old to the adult. This was due to an increase in E at 35C. Dry C at 35C is not significantly different from that at 30C, indicating that the increased C at 35C is due to evaporation. Others

(Richards, 1970; Murrish, 1970) have reported a similiar increase in C at the upper critical temperature and have suggested that it could be due to an increase in peripheral blood flow resulting from increased vasodilation along with increased respiratory evaporation.

Steady-state thermal balance is determined by:

$$M \pm S - E \pm R \pm C = 0 \qquad (15)$$

where,

M = metabolic heat production

S = body heat storage

E = evaporative heat transfer

R = radiant heat transfer

C = convective heat transfer

Conductive heat transfer (K) and work (W) are not considered. A "linearity criterion" was proposed by Gagge (1936) which states that when error terms in the above expression are zero, the result of M minus E must be balanced by S, R, and C. If the relationship M - E vs. $T_b - T_a$ is linear, then the difference between T_b and T_a is assumed to be a reliable indicator of S under these test conditions and the animal is in thermal equilibrium. The slope of this line for a given age of bird represents primarily the convective heat transfer between the animal and its environment, with radiative exchange contributing an insignificant amount to the total heat transfer under these test conditions. Table 3 shows the linear regression components for each age and indicates that there is a

significant linear relationship at all ages studied. This suggests that the birds were in thermal equilibrium and also that $T_b - T_a$ is an acceptable indicator of S.

A large fluctuation in the Y-intercept was found from day 1 (-.1346 watt/g x 10^{-2}) and day 6 (.8086 watt/g x 10^{-2}). Adams et al. (1970) suggested that a Y-intercept above 0 could represent an unaccounted-for radiative heat exchange. Y-intercept values below 0 could represent a radiative heat gain from the chamber walls and/or evaporative heat loss which does not contribute to heat loss from the animal. At day 1 and possibly day 3, it is suggested that evaporation could occur at the plumage surface, not contribute to heat loss from the animal and produce the low Y-intercept. From 10 days after hatching there is no change in the Y-intercept value, although it is above zero.

The slopes of each line are plotted in Figure 16 as a function of age. The curve indicates that the major decrease in convective heat transfer occurs between 3 and 18 days after hatching, with no change in the value between 18 and 25 days. This supports the argument that insulative change is a major factor in thermoregulatory development between 6 and 14 days after hatching (Stage II), represented by a slope decrease, and there is no change in insulation between 18 and 25 days (Stage III), when metabolic increases are suggested to be a primary influence. Convective heat transfer is still decreasing significantly after day 45, but

by day 65 there is no difference from the adult transfer value.

III. Thyroid Metabolism

Thyroid hormones are important for the development of homeothermy in birds (Dawson and Evans, 1960; Singh et al., 1968a; Freeman, 1970; Balaban and Hill, 1971; Bobek et al., 1977). In this study, thyroid activity and its relationship to thermoregulatory development was estimated for the bobwhite. Total plasma T_3 and T_4 levels were measured in the adult and immature quail. Thyroid hormones in the bird are loosely bound to blood proteins (Refetoff et al., 1970) and ,therefore, total plasma thyroid hormone concentrations are often used as indicators of free thyroid hormone levels in growing birds (Davison, 1976; Bobek et al., 1977; King et al., 1977; Thommes and Hylka, 1977). Only free T_3 and T_4 are active in animals, however, there are no acceptable, commercially available, RIA tests for measuring free T_3 and T_4 levels. It is possible to measure the level of plasma proteins which bind thyroid hormones in birds and assume that an increase or decrease in plasma protein concentration indicates that more of the total thyroid hormone is bound or unbound, respectively. In the bird, the plasma protein which binds the largest percentage of thyroid hormones is albumin (Ringer, 1976).

An analysis of plasma thyroid hormone levels in the hatching bobwhite showed a tendency for T_3 and T_4 to rise at

581 hours of incubation (Figures 21, 20). This occurred when approximately 25% of the bobwhites had hatched. An increase in plasma thyroid hormones at hatching has been noted by others (Davison, 1976; King et al., 1977; Thommes and Hylka, 1977). At this time, the bird's beak has entered the air sac and it is actively breathing. It is possible that the change in respiratory exchange surfaces from chorioallantoic membrane to lungs and the increase in energy requirement for breathing could stimulate the increase in metabolic rate (Freeman, 1962) seen at hatching. The increased metabolism may result from increased thyroid hormone levels in response to increased TSH levels (Davison, 1976). Davison (1976) suggested that the wet hatchling might be exposed to a cold stress on emerging from the shell and this could stimulate the increased release of TSH. This has also been suggested as a possible reason for the increased thyroid activity at birth in some mammals (Erenberg et al., 1974). It is doubtful if the birds are cold stressed, since the peak in plasma thyroid hormone level occurs before a large number of the birds have hatched and are exposed to a low T_a. Also, the wet bobwhite is exposed to the incubator environment which has 100% relative humidity and a T_a equal to 38C. With reduced evaporative cooling and a high T_a, cold stress cannot be considered as a possible stimulus for the increased thyroid hormone levels. It is possible that another exogenous or an endogenous factor may stimulate the increase in thyroid activity at

this time.

Okon (1978) found that liver glycogen levels in the Japanese quail decreased at hatching and attributed the change to increased use of energy reserves in response to increased metabolism. In mammals, low concentrations of thyroid hormone produce an increase in glycogen synthesis and a higher level increases glycogenolysis (Bernal and Refetoff, 1977). A 3-fold increase in plasma thyroid hormone levels, like that seen in the bobwhite (Figures 17, 18), could contribute to the drop in liver glycogen level in hatchling Japanese quail (Okon, 1978).

Plasma albumin levels in the 1 day old quail are significantly lower than the 21 day old level (Figure 23). This suggests that there is more free, active T_3 and T_4 in the 1 day old quail than in the 21 day old bird. Whether the high T_3-T_4 levels are due to increased hormone production or decreased utilization is unknown, because it was not possible to test such a small animal for biological half-lives.

No significant changes in plasma T_4 levels were found after day 1. Because T_3 is considered by many to be the active thyroid hormone (Oppenheimer et al., 1972; Ringer, 1976; Slivastava and Turner, 1976b; Bernal and Refetoff, 1977; Oishi and Konishi, 1978) and it changes significantly with quail growth, it will be the central issue for the remainder of this discussion.

In the bobwhite, there is no significant increase in

plasma T_3 levels until between 21 and 29 days after hatching (Figure 18). The plasma T_3 reaches a plateau at approximately 600 ng% (a 100% increase over the 21 day old and adult level) and remains at this level through 65 days after hatching. No significant increase in plasma albumin level occurs from day 21 to day 43 after hatching (Figure 23), suggesting that there is a rise in free, active T_3. In fact, the plasma albumin level of the adult quail is significantly higher than that of the 43 day old quail, although the plasma T_3 level is lower. This implies that there is a higher level of free T_3 in the 43 day old bird than in the adult. Others have reported similiar changes in thyroid activity after hatching. Bobek et al. (1977) found that plasma T_3 levels in the chick increased 1 to 2 weeks after hatching. Singh et al.(1968b) found that the T_4 secretion rate in the chick increased from 4.5 to 5.5 weeks after hatching and decreased between 7 and 56 weeks (Singh et al., 1967).

A common problem in measuring only hormone levels is related to whether the change in the particular level is due to a change in its production or a change in its rate of utilization. By measuring hormonal half-life, it is possible to determine if an increase in plasma thyroid hormone level is due to an increase in its production or a decrease in its uptake. These are two completely opposite interpretations. The biological half-lives of T_3 and T_4 do not change from 21 to 43 days after hatching (Figure 22)

which suggests that there is no increase in the utilization and breakdown of either hormone over this time. The rise in plasma T_3 levels from day 21 to day 45 must be due to an increase in hormone production, either by increased thyroid gland output or increased peripheral conversion of T_4 to T_3. Currently the peripheral conversion of T_4 to T_3 is believed to be a major avenue for T_3 production (Braverman et al., 1970; Astier and Newcomer, 1978; Campbell, 1979). Such a conversion is suggested by the rise in the T_3/T_4 ratio at 29 days of age (Figure 24).

The increase in the plasma T_3 level of the bobwhite (Figure 18) corresponds with the increase in growth rate 21 days after hatching (Figure 2). The increase in daily weight gain could be due to increased thyroid activity. Avian growth is influenced by thyroid activity. When thyroid activity is reduced, there is a decrease in muscle weight gain (King and King, 1976) and total body growth (Mellen and Hill, 1953; Marks and Lepore, 1968; Singh et al., 1968a; Rahja and Snedecor, 1970). Such reductions in growth result from lowered food consumption (King, 1969; Rahja and Snedecor, 1970).

Thyroid activity also affects animal metabolism. In this study, plasma T_3 levels increase (Figure 18) at approximately 25 days after hatching, when the quail is increasing its ability for metabolic heat production at low T_as (Figure 9). The increase in T_3 concentration could be responsible for the metabolic increase, although further

tests are required to establish such a relationship. Bobek et al. (1977) found a high correlation between high plasma T3 levels and the maximum oxygen consumption reached in young chicks at 1 to 2 weeks of age. A similiar relationship between thyroid hormone levels and metabolic heat production was found in nestling vesper sparrows (Dawson and Evans, 1960) and neonatal chicks (Singh et al., 1968a). Also, Spiers et al.(1974) found that thyroid activity in the Japanese quail closely paralleled thermoregulatory development. Others have found that an increase in thyroid hormones produces an increase in heart rate in the chicken (Shimada and Oshima, 1973; Klandorf et al., 1978). Such an increase could increase both heat and nutrient distribution to the tissues. The increased energy supply to the tissues could provide for increased metabolic heat production at low T_a.

Summary

1. The steady-state thermoregulatory responses of the immature (1, 3, 6, 10, 14, 18, 25, 45 and 65 day old) and mature bobwhite were examined at 10, 15, 20, 25, 30 and 35C.
2. Growth and thermoregulatory development in the bobwhite was divided into 3 stages. These stages included day 1 to day 6 (Stage I), day 6 to day 14 (Stage II) and day 14 to the adult (Stage III).
3. Stage I
   a. There was limited increase in body mass and plumage growth.
   b. The bobwhite was not able to maintain a stable internal body temperature (T_b) above T_a at T_a 20C or lower. Internal body temperature at T_a 25 or 30C increased as a function of age, but did not reach adult T_b.
   c. Metabolic heat production increased from 1.5 watt/g x 10^{-2} at day 1 to 2.4 watt/g x 10^{-2} at day 6, due to replacement of metabolically inactive yolk with metabolically active tissue and a shift in diet from lipid to carbohydrate.
   d. Dry thermal conductance increased approximately

.18 watt/g/C x 10^{-2} from day 1 to day 6, possibly because metabolic heat production increased without an increase in thermal insulation.

e. Total evaporative heat loss increased proportionally (.30 watt/g x 10^{-2}) with an increase in T_a from 25 to 35C, but not as a function of age. The percentage of heat loss by evaporation decreased, although not significantly, with age.

f. The major contributor to the increase in T_i during Stage I was the increase in metabolic heat production.

4. Stage II

a. Plumage quantity increased rapidly during Stage II, as evidenced by the 3-fold increase in the plumage to body mass ratio.

b. Internal body temperature approached the adult T_b at 30 and 35C, but was significantly lower than adult Tb at 25C. The bobwhite was still unable to maintain Tb above T_a at T_a 20C.

c. Metabolic heat production did not increase with age and even decreased .7 watt/g x 10^{-2} at T_a 35C.

d. Thermal insulation increased significantly due to a decrease in the surface area to mass ratio and an increase in plumage quantity.

e. Total evaporative heat loss did not change significantly.

f. The major contributor to the increase in T_i during Stage II is the increase in thermal insulation.

5. Stage III

a. Growth rate changed from 1.7 g/day before day 20 to 2.8 g/day afterwards.

b. The major decrease in surface area to mass ratio occurred before day 20.

c. At 18 days after hatching, metabolic heat production at 25C was .5 watt/g x 10^{-2} above the 30C level. Increases in metabolic heat production allowed the bird to maintain a significant separation of the T_b-T_a interval at 35, 30, 25 and 20C.

d. At 25 days after hatching, metabolic heat production progressively increased 1.0 watt/g x 10^{-2} with a decrease in T_a from 25C to 15C.

e. After day 25, there was a parallel, age-dependant decrease in metabolic heat production as a function of age. This was probably due to an increase in thermal insulation after day 25.

f. Total evaporative heat loss and the percentage of heat loss by evaporation did not change significantly as a function of age.

g. The major thermoregulatory changes in Stage III included a maintained increase in metabolic heat production at T_a's below 25C and a continued increase in thermal insulation which reduced the

requirement to increase metabolic heat production above the 6 day-old level for any given T_a.

6. Several changes in thyroid metabolism occurred from 1 to 65 days after hatching which could have affected metabolic heat production in the bobwhite.
   a. Plasma T_3 and T_4 levels increased 3-fold at hatching. This increase might provide the necessary rise in metabolism required for the bird to emerge from the egg.
   b. There was no significant change in plasma T_4 levels after day 10. Plasma T_3 increased significantly (300ng% to 600ng%) from 21 to 29 days after hatching and remained above the adult level (300ng%) through 65 days after hatching.
   c. The half-life of plasma T_3 was significantly lower (3.2hr) at 21 and 45 days after hatching than in the adult (5.0hr), indicating that more T_3 was being produced from 21 to 45 days after hatching than by the adult.
   d. An increase in T_3 production could have contributed to the ability of the 25 day old to maintain a stable metabolic heat production at T_a 15C.

APPENDICES

APPENDIX 1

JUNE-JULY VIVARIUM

TEMPERATURE

APPENDIX 1

JUNE-JULY VIVARIUM

TEMPERATURE

The June-July vivarium temperatures (ordinate: C; T_a) are presented as functions of the June-July dates (abscissa: Day) in Figure A1.

Figure A1. June-July vivarium temperature.

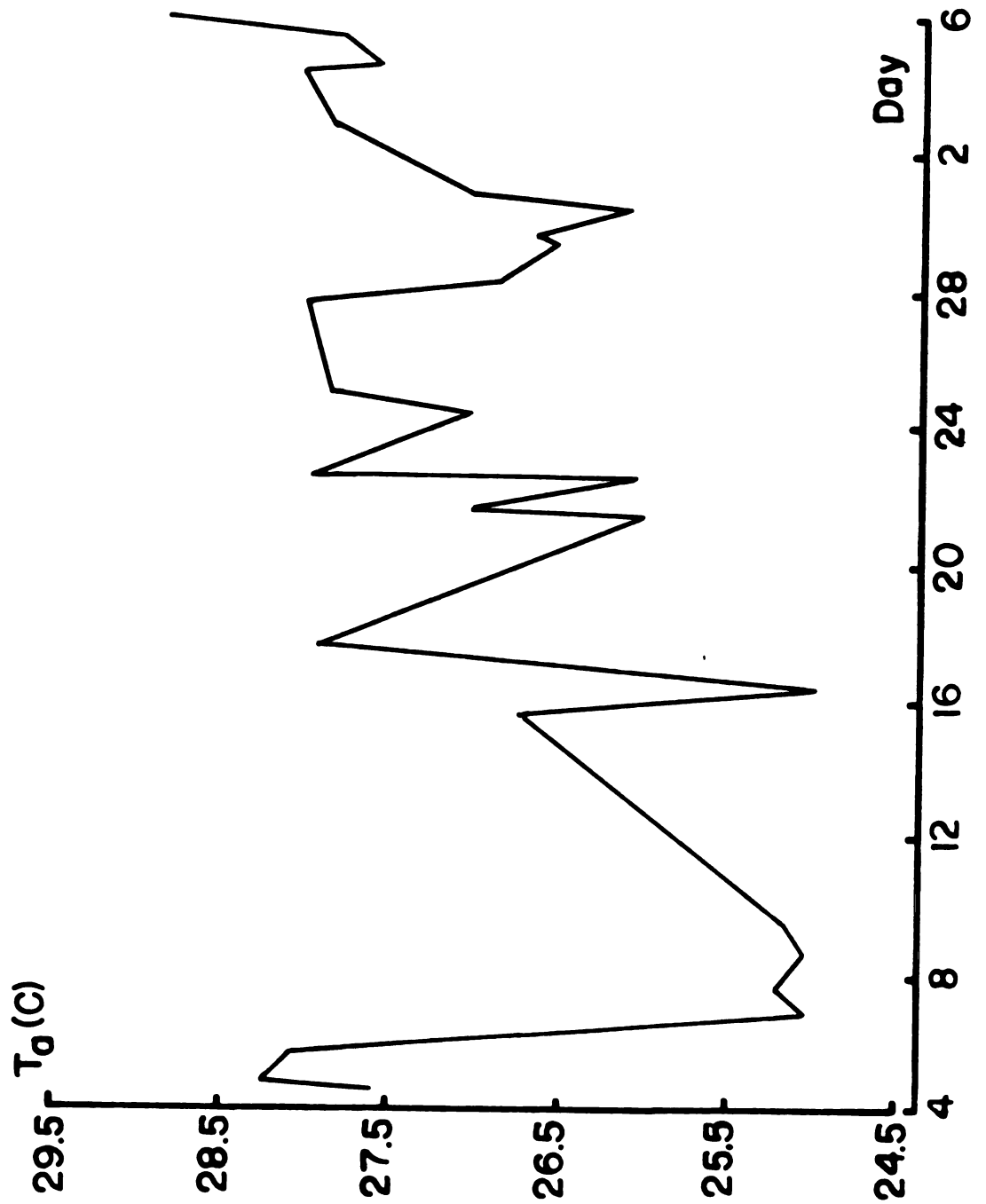


Figure A1.

APPENDIX 2

DECEMBER-JANUARY

VIVARIUM TEMPERATURE

APPENDIX 2

DECEMBER-JANUARY
VIVARIUM TEMPERATURE

The December-January vivarium temperatures (ordinate: C; T_a) are presented as functions of December-January dates (abscissa: Day) in Figure A2.

Figure A2. December-January vivarium temperature.

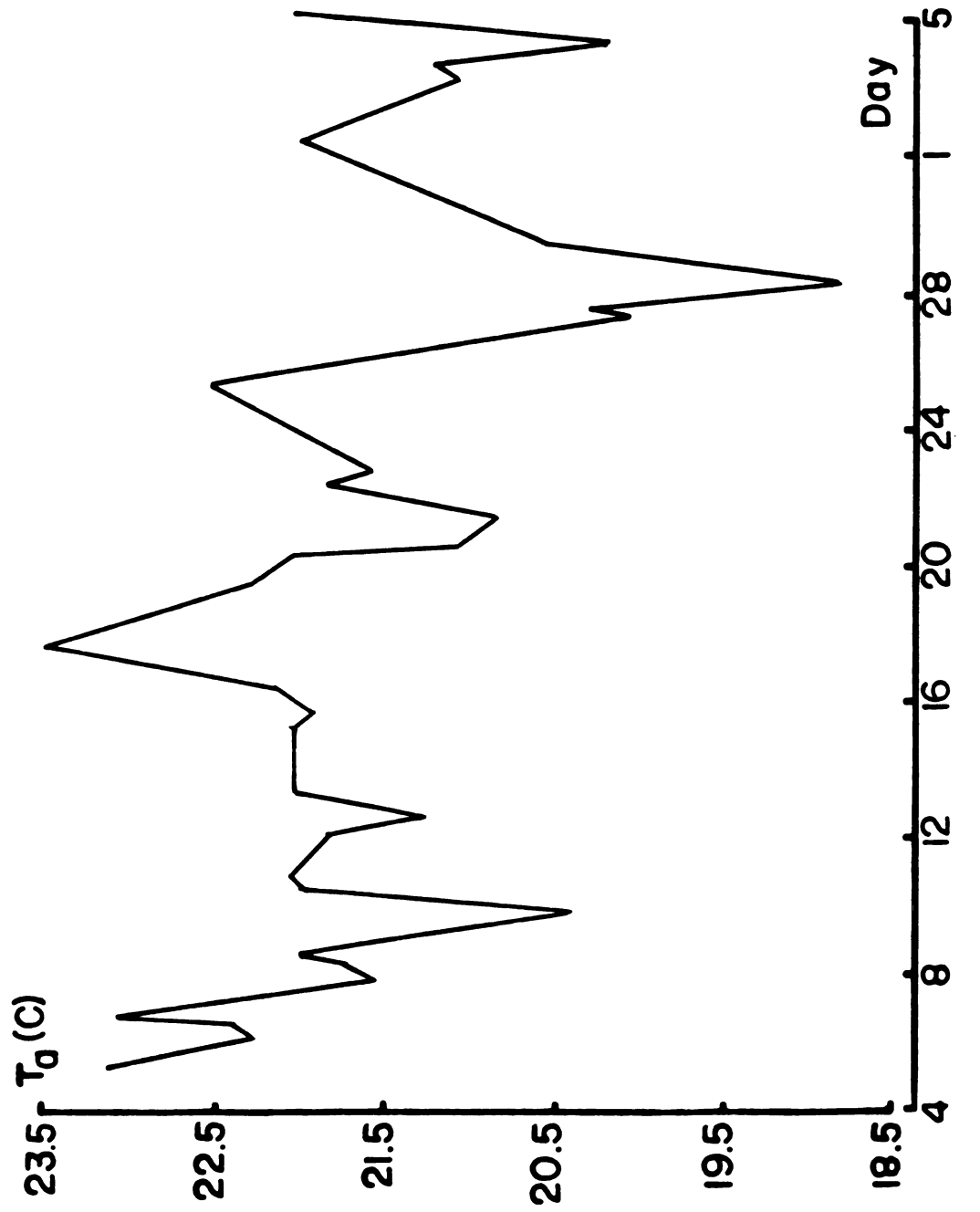


Figure A2.

APPENDIX 3

QUAIL DIETS

APPENDIX 3

QUAIL DIETS

		MSU 72-15 Starter	MSU 72-16 Breeder
1.	Protein--g/g diet	0.29	0.235
2.	Metabolizable energy--kcal/g	3.02	2.880
3.	Percent calcium	1.02	2.750
4.	Percent phosphorus	0.65	0.530
5.	Percent fat	8.20	8.400
6.	Percent fiber	3.20	3.100
7.	Iodized salt--g/kg	3.50	3.800

APPENDIX 4

EFFECT OF DIET CHANGE

APPENDIX 4

EFFECT OF DIET CHANGE

Procedure:

Five adult male quail were fed MSU 72-15 Quail Starter Diet and five adult male quail were fed MSU 72-16 Quail Breeder Diet for 34 days to test the effect of MSU Quail Starter Diet on the adult quail. Quail body mass was measured before and after the experiment by weighing the quail on a Mettler Toploader balance to the nearest .Ø1g (Table A1). All birds were killed by cervical dislocation and adrenal glands were removed for wet mass measurements. Excess water was removed from each adrenal gland with a section of filter paper and then weighed on a Mettler Preweigh balance to the nearest .ØØØ1g. Any difference between control and experimental group adrenal masses served as a determinant of stress produced by MSU 72-15 Quail Starter Diet (Table A1).

Table A1. Results of diet change

	Control Breeder Diet (g)	Experimental Starter Diet (g)
Mean Body Mass (Before)	185.8 ±5.4	179.8 ±5.7
Mean Body Mass (After)	186.2 ±5.9	185.6 ±5.5
Mean Adrenal Mass	.0036 ±.0003	.0028 ±.0003

Mean ±SE; n = 5

There was no significant difference ($p \leq 0.01$), using Student's t Distribution, between control and experimental values. Quail fed MSU 72-15 Quail Starter Diet had a 5.6g ±2.0 increase in body mass, whereas the quail fed MSU 72-16 Quail Breeder Diet increased body mass by only .4g ±.9.

APPENDIX 5

WATER-DISPLACEMENT TECHNIQUE FOR FLOWMETER CALIBRATION

APPENDIX 5

WATER-DISPLACEMENT TECHNIQUE FOR FLOWMETER CALIBRATION

Procedure:

Three vertical glass flowmeters, Model Number 2C, 3C and 4C (Scientific Glass Apparatus Co., Inc., Bloomfield, New Jersey), were calibrated for both steel and glass ball positions by determining the rate at which water free, room temperature air displaced water from a container. A 1 liter graduated cylinder was filled with water and inverted in a 4 liter beaker containing 2 liters of water. A section of 5/16 inch diameter Tygon tubing (Tygon Tubing, Norton Plastics and Synthetics Division, Akron, Ohio) was used to connect the air pump to the flowmeter and a second section of tubing ran from the flowmeter, under the inverted graduated cylinder and up pass the cylinder water level. The time required to fill a specific volume of the graduate cylinder with air, at a constant flowrate, was measured. Water and air pressures within the graduated cylinder were maintained constant during calibration by raising the graduated cylinder as it filled with air.

Results:

Calibration curves (Figures A3, A4, A5, A6, A7, A8) are presented at both glass and steel ball positions for 2C, 3C, and 4C flowmeters with flowrate (ordinate: cc/min; V) as a function of flowmeter divisions (abscissa: cm).

Figure A3. Calibration of Tube 2C for air (glass ball).

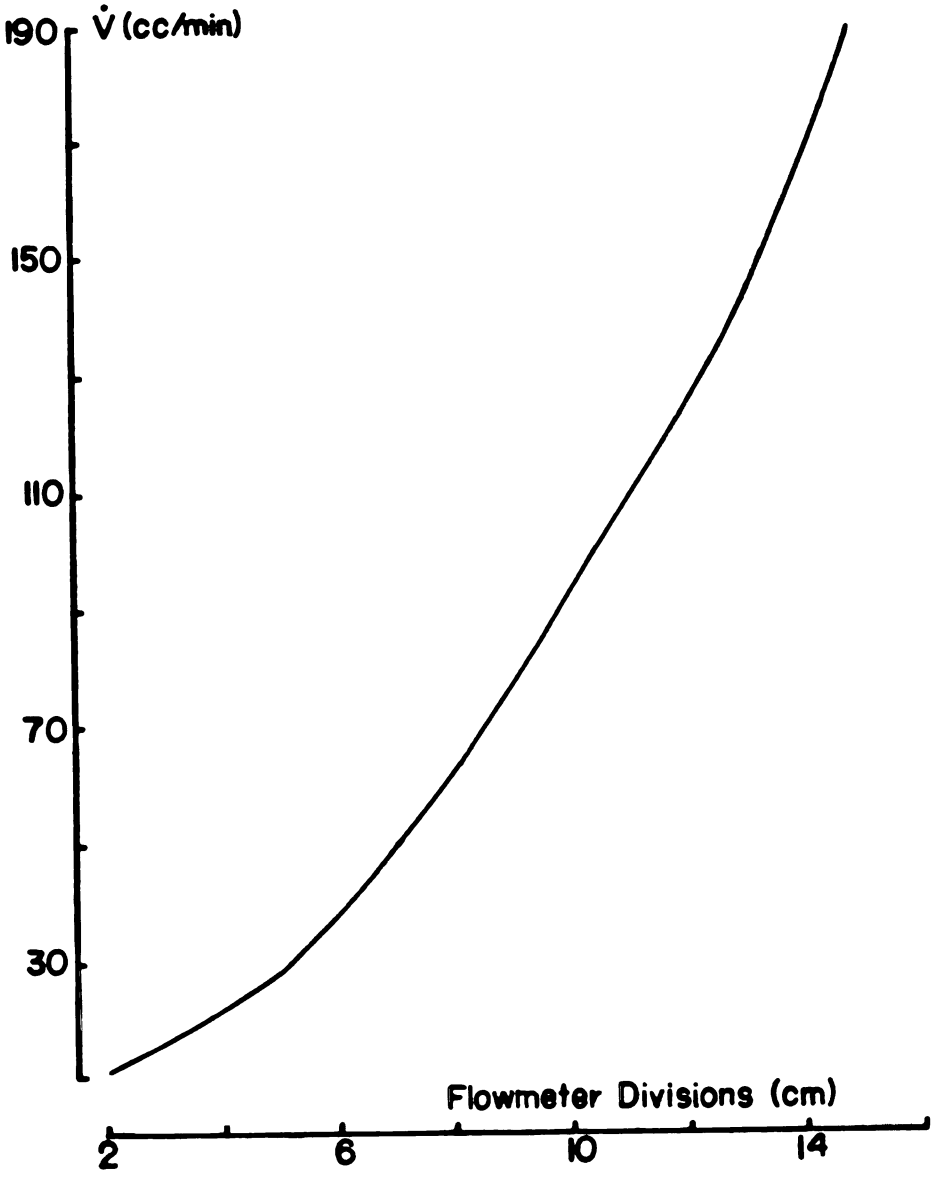


Figure A3

Figure A4. Calibration of Tube 2C for air (steel ball).

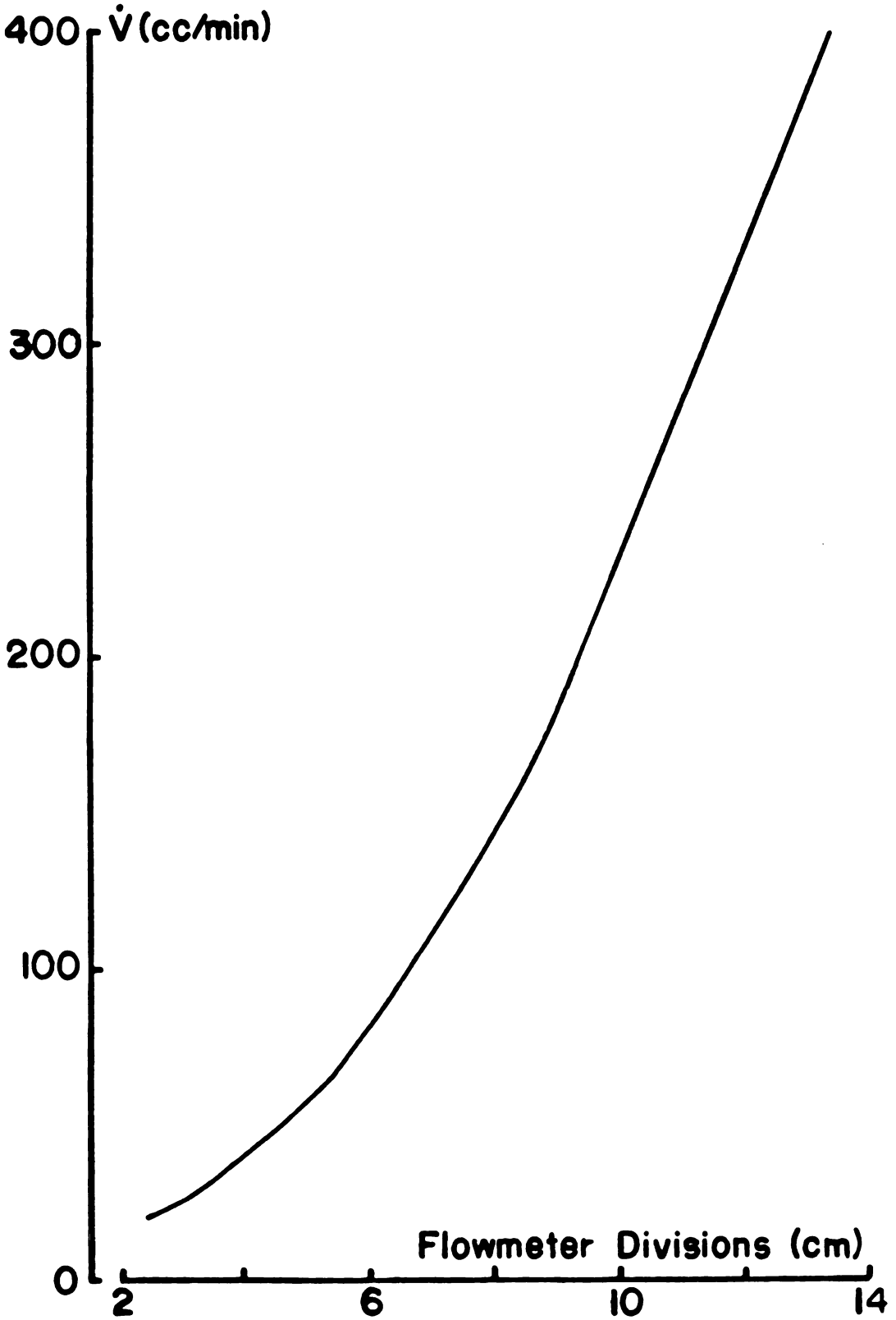


Figure A4

Figure A5. Calibration of Tube 3C for air (glass ball).

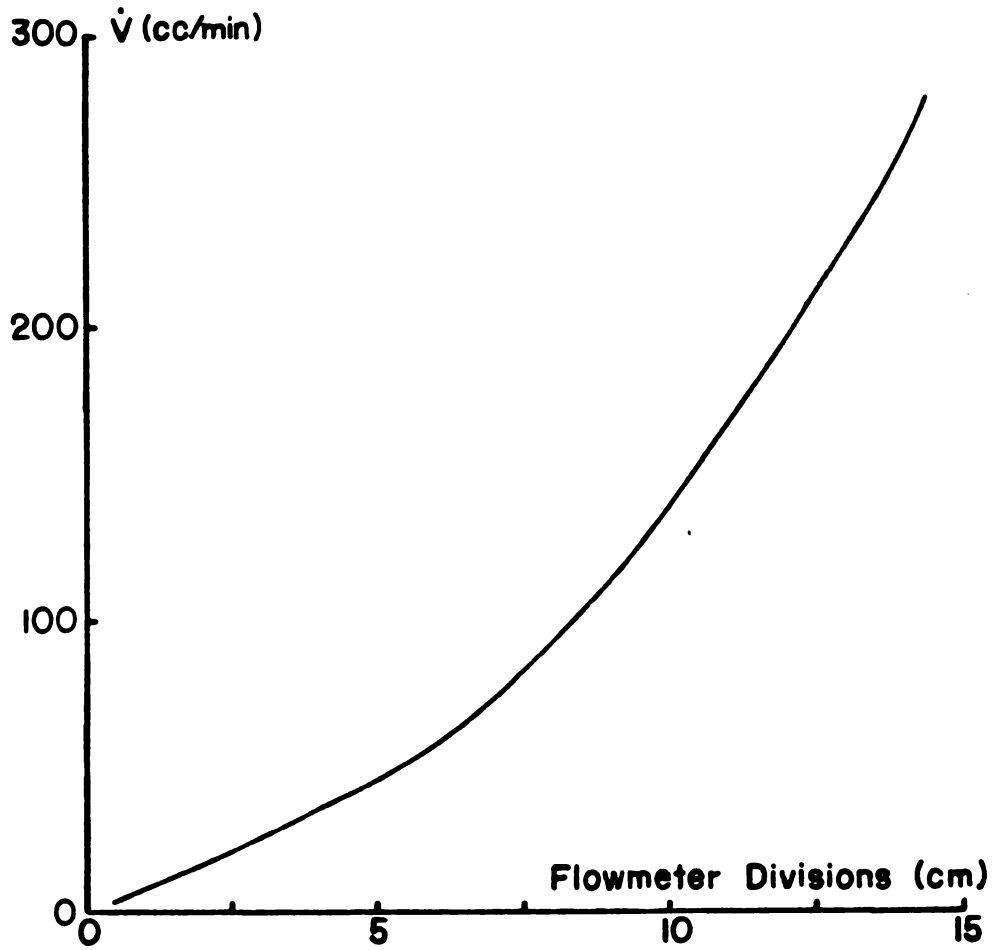


Figure A5

Figure A6. Calibration of Tube 3C for air (steel ball).

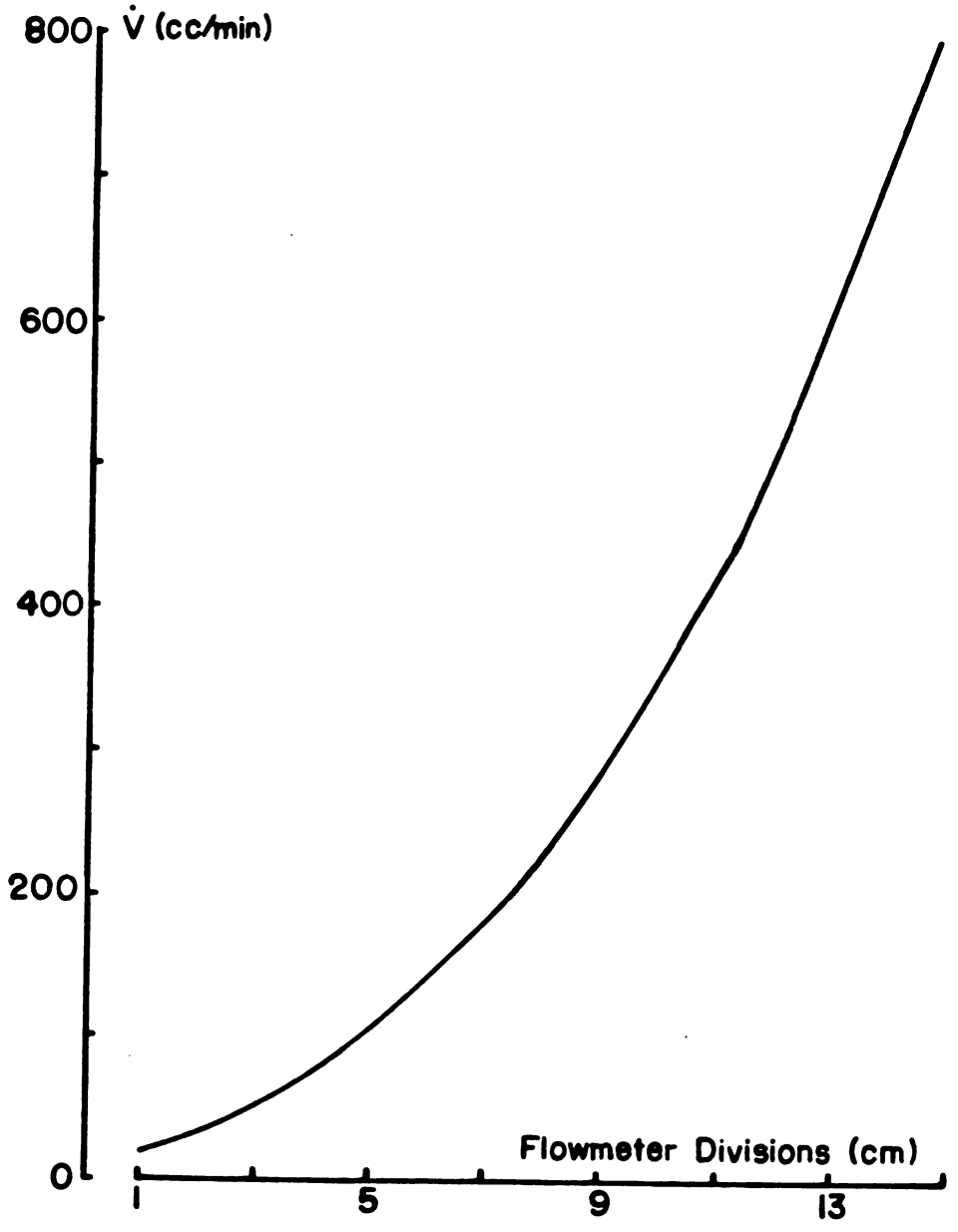


Figure A6

Figure A7. Calibration of Tube 4C for air (glass ball).

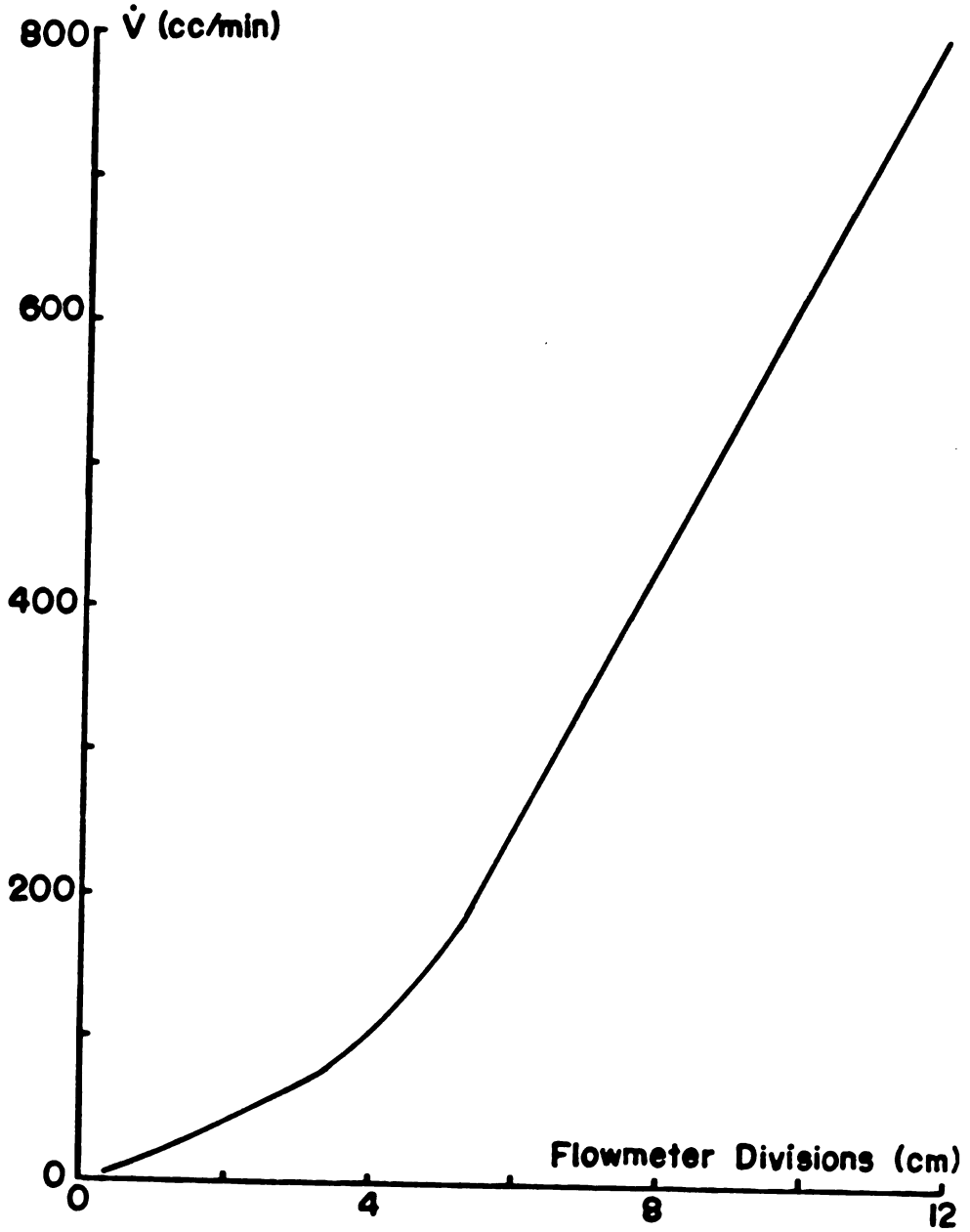


Figure A7

Figure A8. Calibration of Tube 4C for air (steel ball).

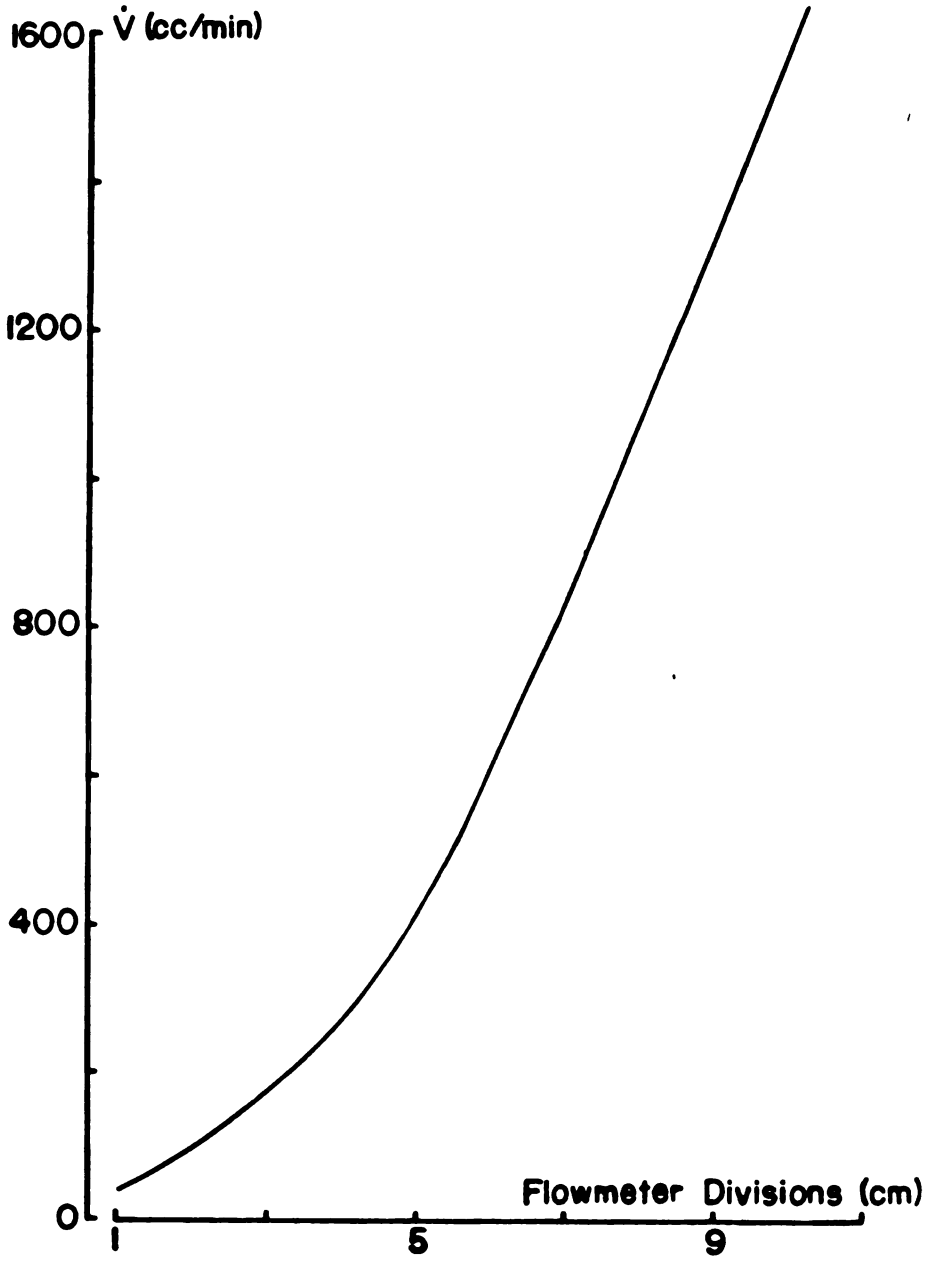


Figure A8

APPENDIX 6

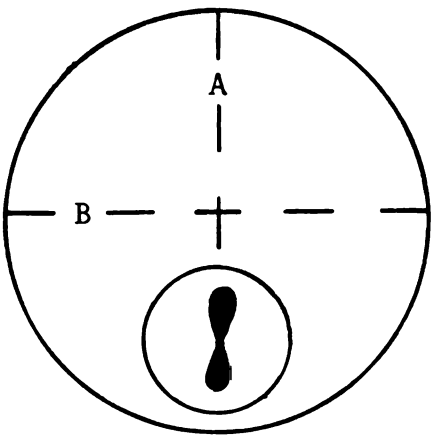
TEMPERATURE PROFILES IN METABOLIC CHAMBER

APPENDIX 6

TEMPERATURE PROFILES IN METABOLIC CHAMBER

Procedure:

Temperature profiles were determined for the empty air chamber with the fan turned on. Air flowrate was maintained at 450 ml/min and at mean chamber temperatures of 11.45, 20.67, 29.00, or 38.87C during calibration. The following figures show isothermal lines at .125C intervals through two planes, perpendicular to each other within the chamber. Plane A passed through both the chamber cylinder diameter and fan cylinder diameter. Plane B was at a right angle to Plane A.



Each plane contained nine, 40-gauge thermocouples placed at the indicated locations in Figure A9 through Figure A16. All temperatures are steady-state values. All other temperatures were estimated by interpolation.

Results:

The largest temperature difference was between the lower center and upper rim of the chamber at all test temperatures. The following temperature extremes were recorded at each calibration temperature:

Mean Chamber Temperature (C)	Maximum Range (C)
38.87	± .62
29.00	± .25
20.67	± .07
11.45	± .65

Figure A9. Metabolic chamber thermal isobars at 11.45C through plane A. Drawing is to scale (1:1), with the solid line indicating air chamber boundaries. The lower 2.5 cm represent the space below the hardware cloth.

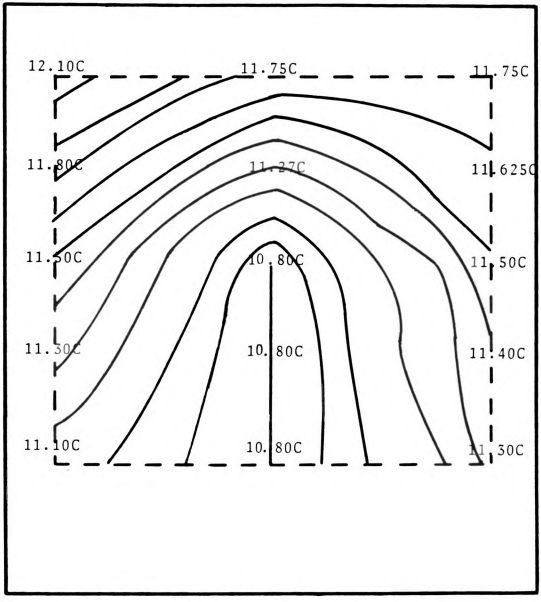

12.10C
11.75C
11.75C
11.80C
11.27C
11.625C
11.50C
10.80C
11.50C
11.30C
10.80C
11.40C
11.10C
10.80C
11.30C

Figure A9

Figure A10. Metabolic chamber thermal isobars at 11.45C through plane B. See Figure A9.

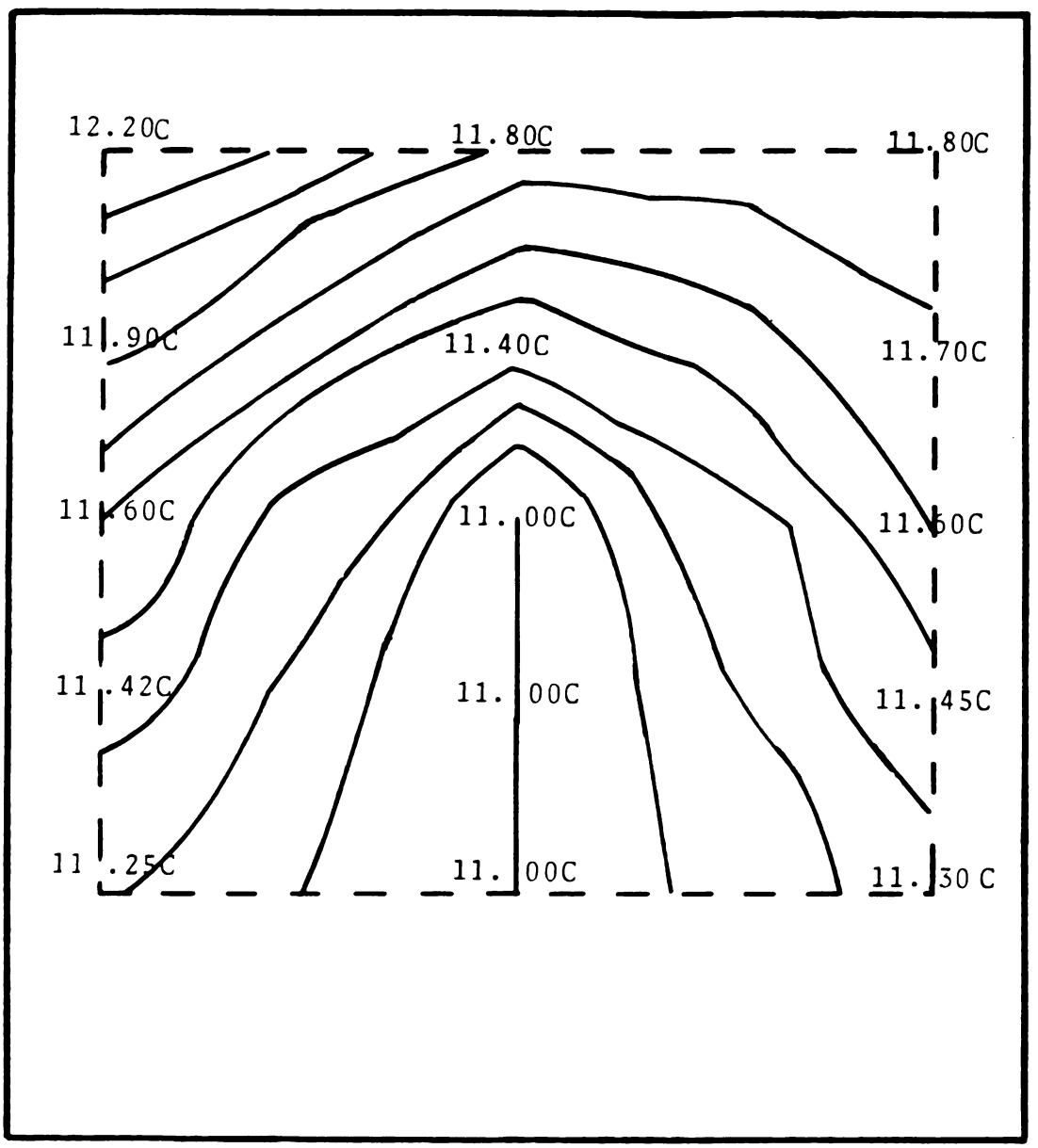

12.20C
11.80C
11.80C
11.90C
11.40C
11.70C
11.60C
11.00C
11.60C
11.42C
11.00C
11.45C
11.25C
11.00C
11.30C

Figure A10

Figure A11. Metabolic chamber thermal isobars at 20.67C through plane A. See Figure A9.

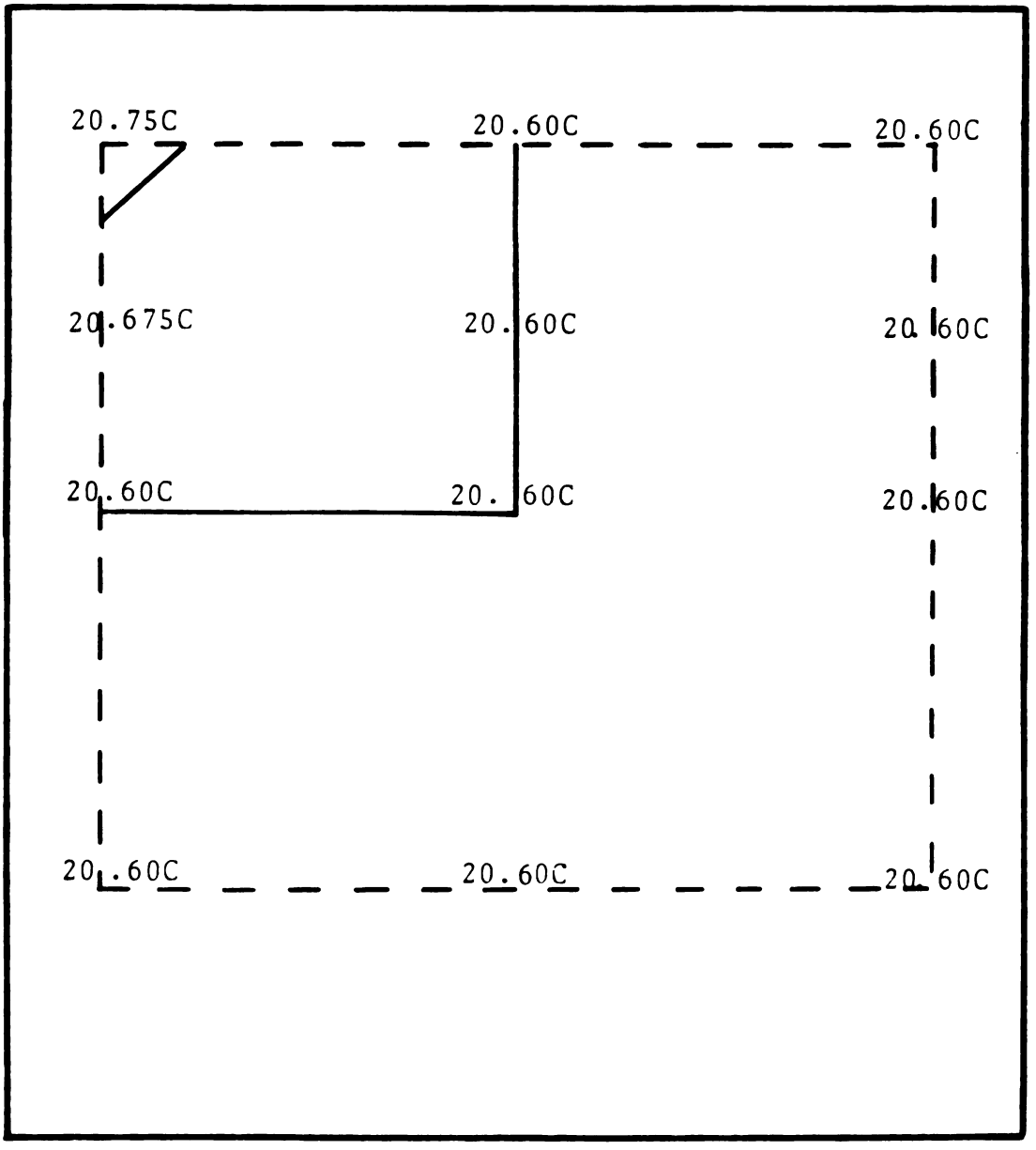

20.75C
20.60C
20.60C
20.675C
20.60C
20.60C
20.60C
20.60C
20.60C
20.60C
20.60C
20.60C

Figure A11

Figure A12. Metabolic chamber thermal isobars at 20.67C through plane B. See Figure A9.

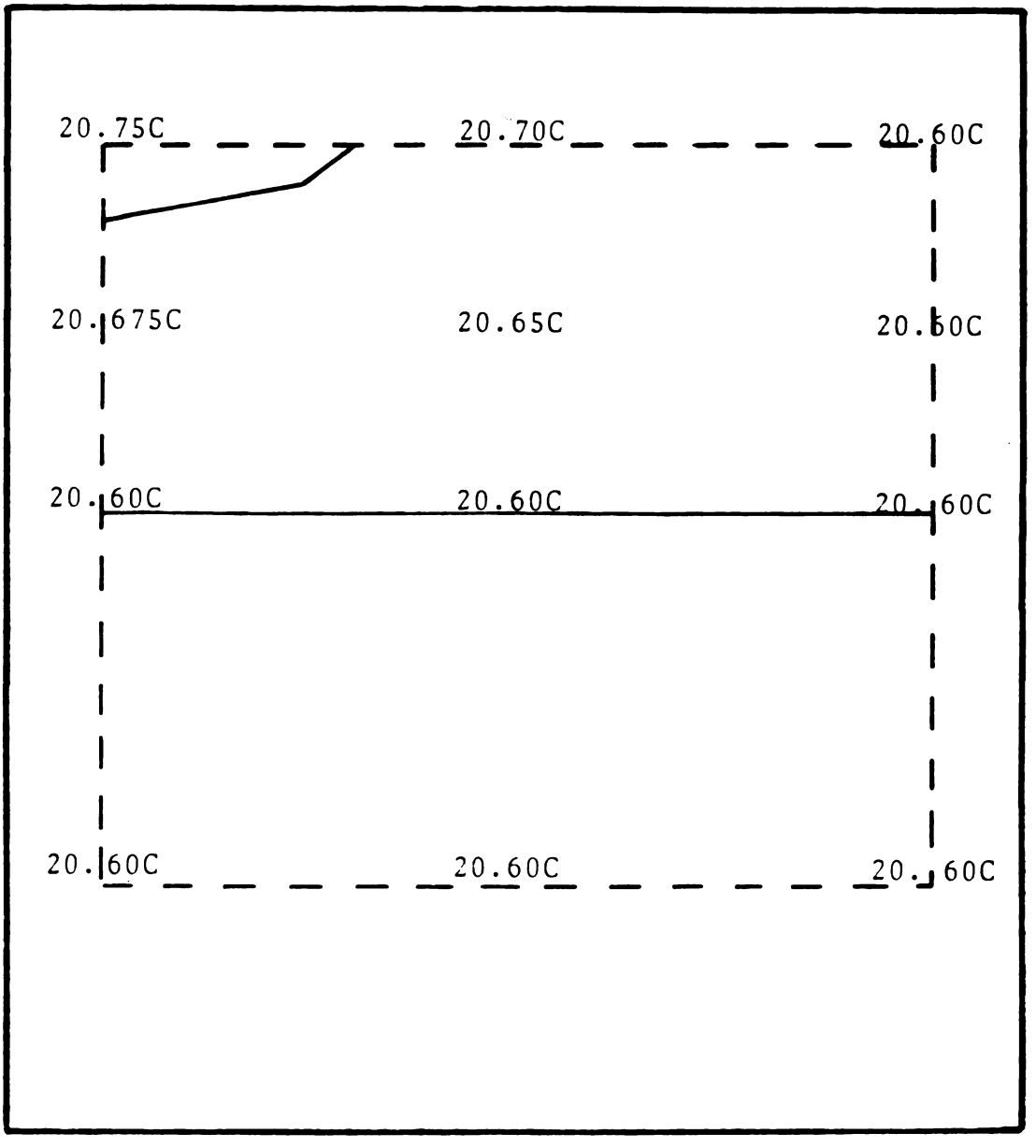

20.75C
20.70C
20.60C
20.675C
20.65C
20.60C
20.60C
20.60C
20.60C
20.60C
20.60C
20.60C

Figure A12

Figure A13. Metabolic chamber thermal isobars at 29.00C through plane A. See Figure A9.

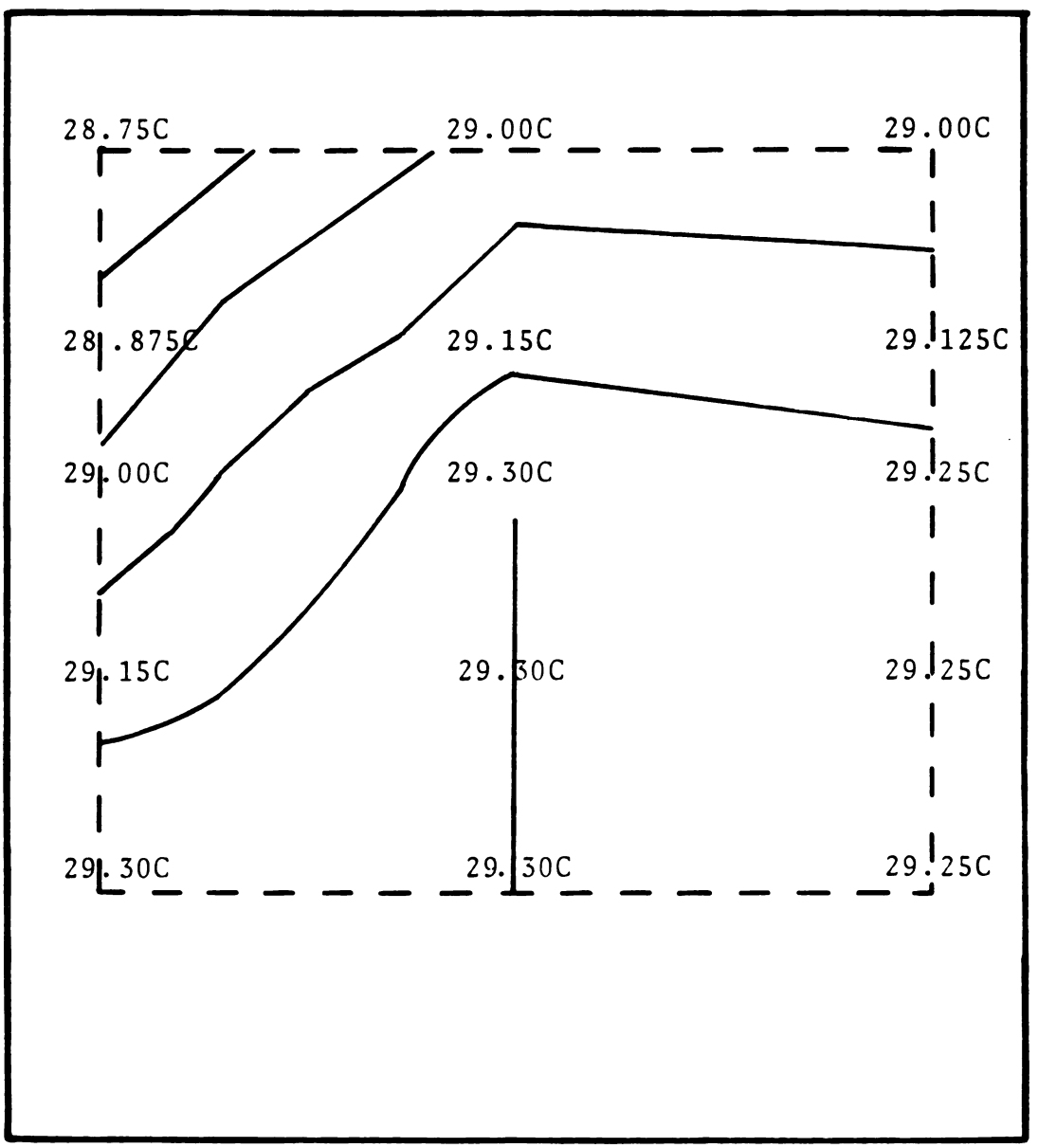

28.75C
29.00C
29.00C
28.875C
29.15C
29.125C
29.00C
29.30C
29.25C
29.15C
29.30C
29.25C
29.30C
29.30C
29.25C

Figure A13

Figure A14. Metabolic chamber thermal isobars at 29.00C through plane B. See Figure A9.

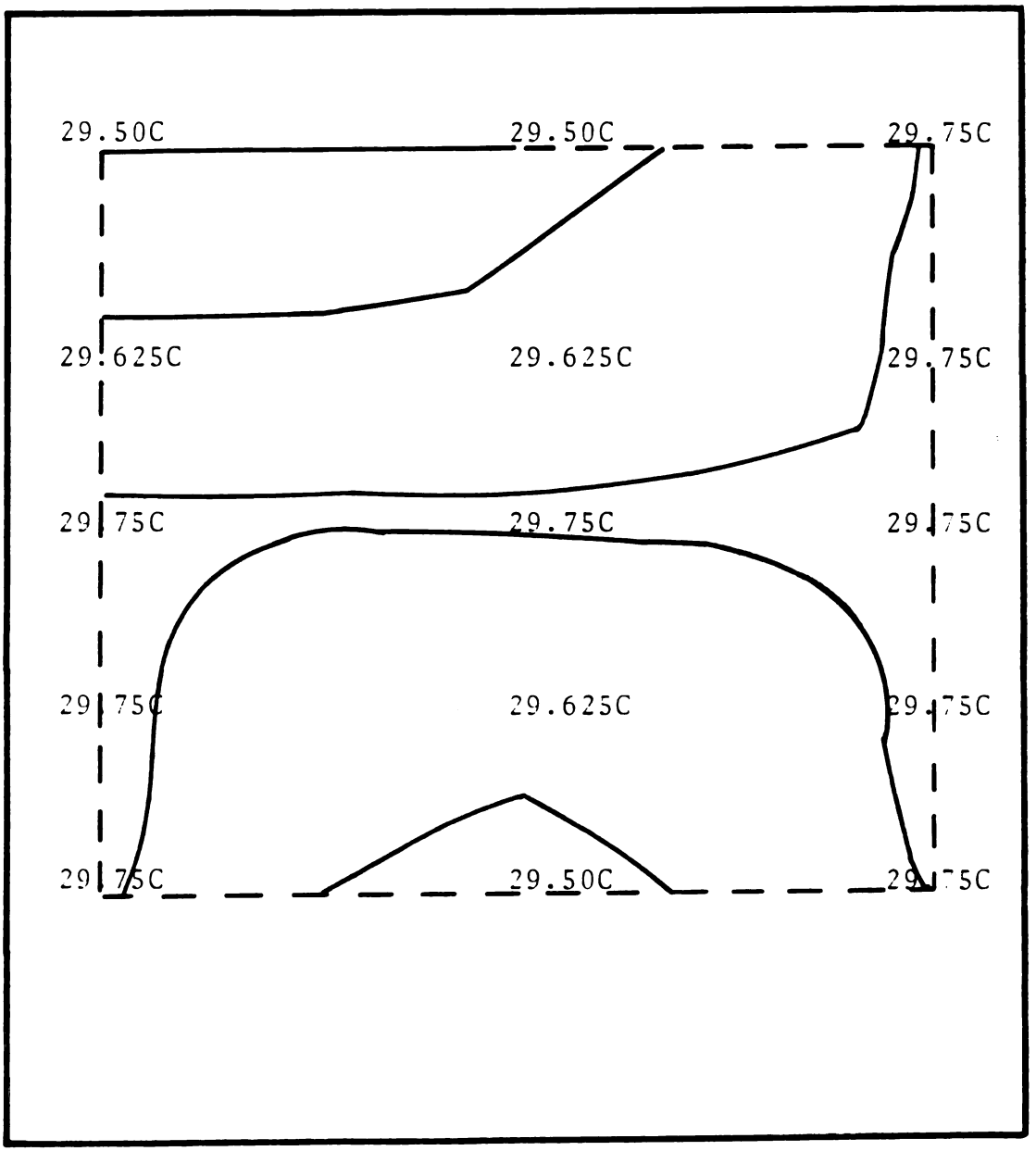

29.50C
29.50C
29.75C
29.625C
29.625C
29.75C
29.75C
29.75C
29.75C
29.75C
29.625C
29.75C
29.75C
29.50C
29.75C

Figure A14

Figure A15. Metabolic chamber thermal isobars at 38.87C through plane A. See Figure A9.

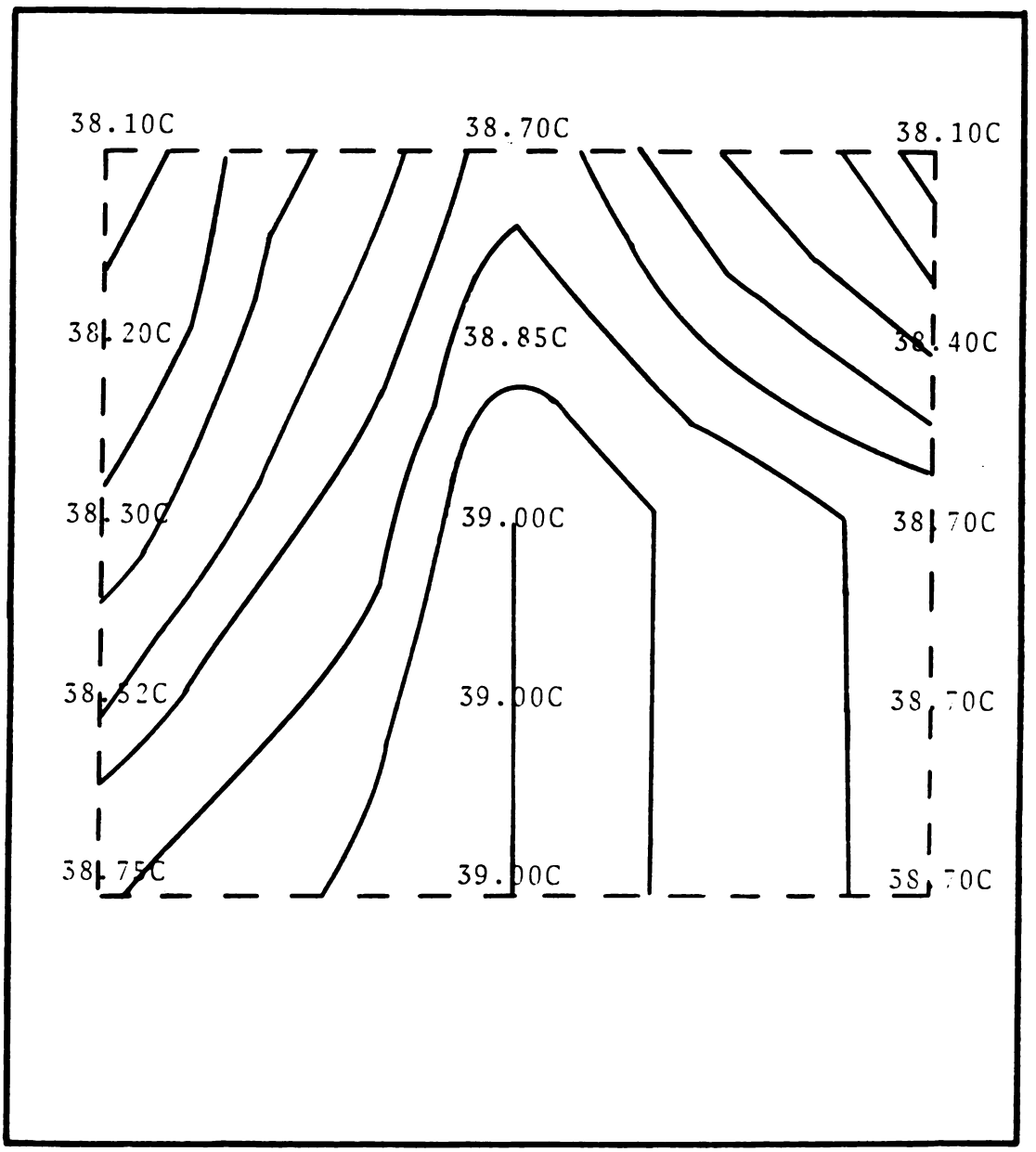

38.10C
38.70C
38.10C
38.20C
38.85C
38.40C
38.30C
39.00C
38.70C
38.52C
39.00C
38.70C
38.75C
39.00C
38.70C

Figure A15

Figure A16. Metabolic chamber thermal isobars at 38.87C through plane B. See Figure A9.

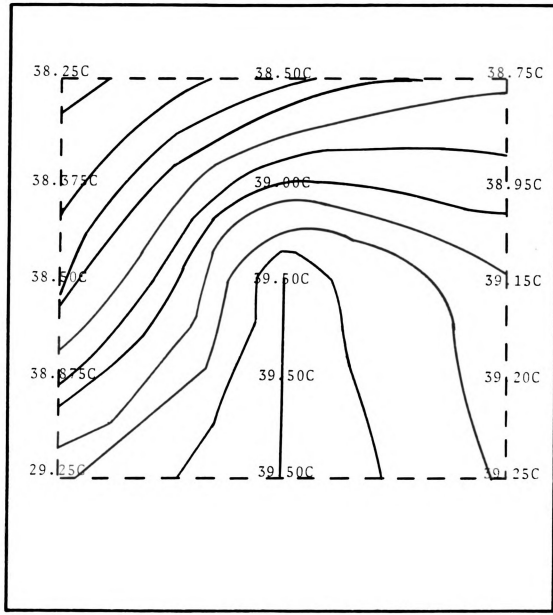

38.25C
38.50C
38.75C
38.87SC
39.00C
38.95C
38.50C
39.50C
39.15C
38.87SC
39.50C
39.20C
29.25C
39.50C
39.25C

Figure A16

APPENDIX 7

OXYGEN CONTENT ANALYSIS

APPENDIX 7

OXYGEN CONTENT ANALYSIS

Reference: Instruction Manual, Model F3 paramagnetic oxygen analyzer, Beckman Instruments, Inc., Fullerton, California

Principle:

Oxygen is a highly paramagnetic gas, compared to other atmospheric gases, and has the ability to acquire magnetic properties when placed in a magnetic field. The oxygen analyzer determines the oxygen partial pressure of the gas sample by measuring the ability of the sample to become magnetized. Gas analysis is conducted in a compartment which contains a dumbbell-like object that is suspended from a quartz fiber, located in a nonuniform magnetic field. The two spherical portions of the dumbbell are exposed to forces which are a function of the magnetic susceptibility of the spheres and the surrounding gas. As the partial pressure of oxygen in the gas sample increases, the force on each sphere increases. The increased force causes an increased displacement of the spheres from their null position in the magnetic field. A wedge-shaped mirror is positioned in the center of the dumbbell and reflects a

light beam which is sent from an exciter lamp. The mirror position changes as the dumbbell moves and alters the direction of the reflected light beam. The beam is then split and each portion is sent to one of a matched pair of phototubes. Both phototubes are connected in series to a voltage divider. The resistance in each phototube is inversely proportional to the intensity of the impinging light beam and they are unequal when the mirror moves. The voltage which develops between the two phototubes and ground is received by an amplifier circuit and registered on a meter.

APPENDIX 8

CARBON DIOXIDE ANALYSIS

APPENDIX 8

CARBON DIOXIDE ANALYSIS

Reference: Instruction Manual, Medical Gas Analyzer LB-2, Beckman Instruments, Inc., Anaheim, California

Principle:

The LB-2 operates on the principle that certain gases, such as carbon dioxide, are able to absorb energy from a particular portion of the infrared spectrum. Two infrared sources are located within the analyzer, with one beam passing through a CO_2 reference cell and the other through the sample cell. Each infrared beam passes from a cell into one of two compartments, located in the detector cell, which is separated by a metal diaphragm. Gas molecules within the detector cell increase vibration as more infrared radiation is received by the compartment. This produces an increase in pressure within that compartment. If there is no CO_2 in the sample cell, the pressures in both compartments are identical and the diaphragm is stationary. When CO_2 is present in the sample cell, it absorbs a portion of the infrared energy that is directly proportional to the amount of CO_2 in the gas sample. The amount of infrared radiation reaching the

detector cell is reduced and the pressure is lowered. This causes the diaphragm to bend and changes the capacitance between itself and a fixed plate in the detector cell. The analyzer then processes the signal from the detector cell to yield an output signal which is directly proportional to the percentage of CO_2 in the air sample.

APPENDIX 9

RELATIVE HUMIDITY ANALYSIS

APPENDIX 9

RELATIVE HUMIDITY ANALYSIS

Reference: Humidity Transducer Instruction No. H-170, Hygrodynamics, Inc., Silver Spring, Maryland

Principle:

The humidity transducer operates on the principle that a hygroscopic layer can change its electrical resistance with a change in relative humidity. Eight sensor rods, constructed of a plastic coil with a hygroscopic coating of lithium chloride and/or bromide, are each sensitive to a specific relative humidity range. The voltage output from the sensor is rectified and temperature compensated before being sent to a Moseley Plug-In Unit and Strip Chart Recorder. The relative humidity transducer is sensitive over a range of 10-99%rh with an accuracy of $\pm$3%rh between 4.5C and 49C. In addition, the manufacturer has reported that the transducer can withstand several hundred mph gas velocities.

Calibration:

The transducer is calibrated by pumping air of known percent relative humidity through the transducer and recording the pen deflection of the strip chart recorder.

The transducer was calibrated daily across the Ø-1ØØ%rh range at a sensitivity setting of 2 volts. Fine-point sensitivity adjustments were conducted at the 2 volt setting by inserting a calibration set-plug into the transducer, while it was receiving dry air, and adjusting the fine control knob to obtain a 25 cm. pen deflection. This deflection corresponded to 1ØØ%rh.

The transducer was used at both 2 and 1 volt sensitivity settings. Initially, the transducer was calibrated at both the 1 and 2 volt sensitivity settings, using a wide range of relative humidities. The first step in the calibration procedure was to pass dry air, at a known flow rate, through the calibration vessel (Figure A17). Any selected relative humidity could be produced with the calibration vessel by injecting a specific quantity of water into the dry, air stream.

The basic principle behind the calibration procedure was to inject a known quantity of water into the air until a steady-state pen deflection was achieved. By measuring water loss at a known flowrate, barometric pressure, room temperature and time span, it was possible to calculate the representative percent relative humidity level for the given deflection.

Calculations:

$$\dot{V}_{STPD} = \dot{V}_{ATP} \times (BP/760mmHg) \times [273K/(273K + T_a)]$$

where,

Figure A17. Relative Humidity Calibration Vessel.

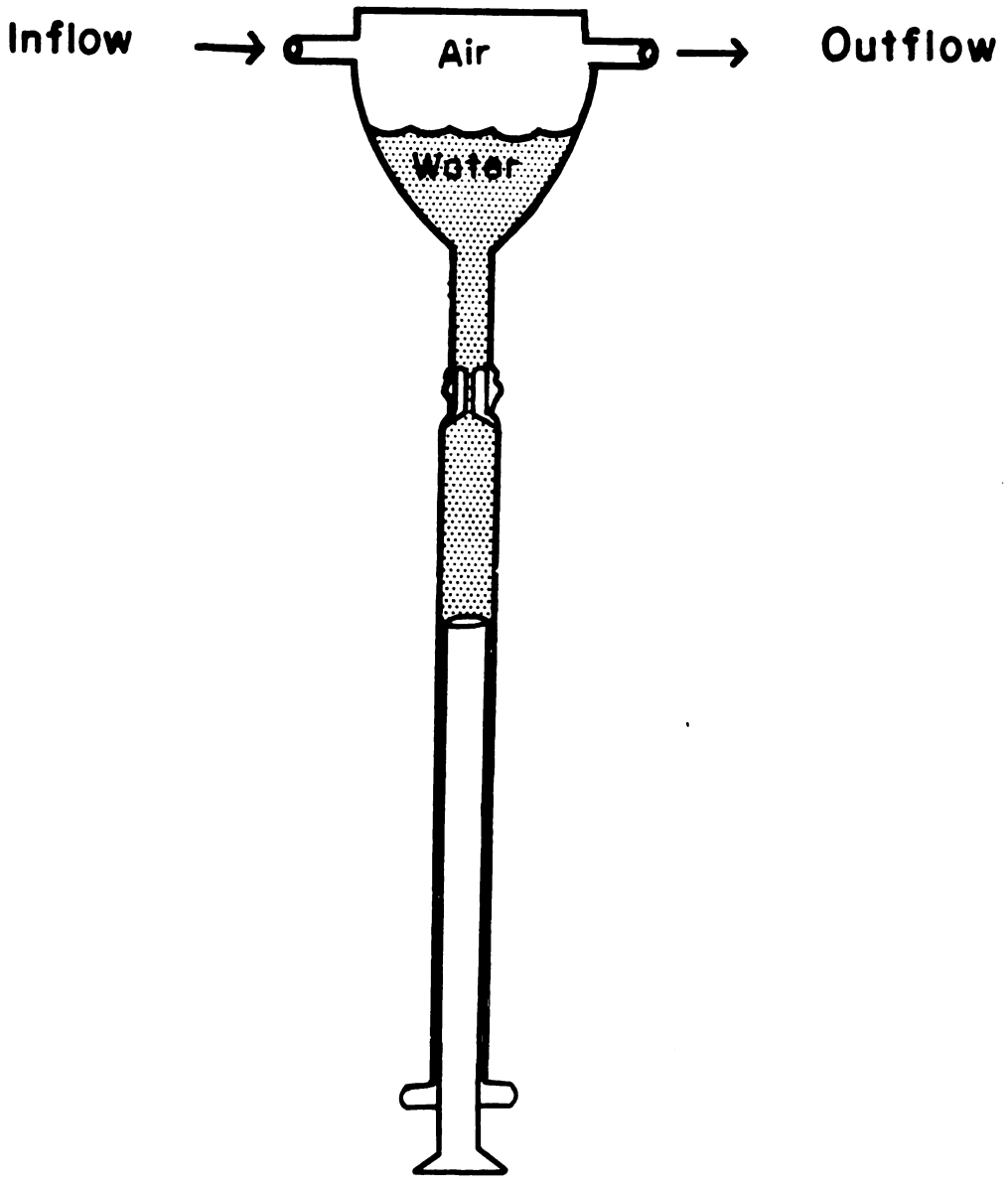


Figure A17

$\dot{V}_{STPD}$ = Air Flowrate at Standard Temperature and

$\dot{V}_{ATP}$ = Air Flowrate at Atmospheric Temperature and Pressure

BP = Room Barometric Pressure (mmHg)

T_a = Room Temperature (C)

A curve was recorded by the strip chart recorder and the area under the curve measured to the nearest .1 cm^2 using a Compensating Polar Planimeter (Keuffel and Esser Co., Detroit, Michigan). The calibration vessel was weighed on a Mettler Balance (Mettler Instrument Corp., Hightstown, N.J.) to the nearest 1.0×10^{-4}g, before and after the test, to determine the amount of water loss. The quantity of water represented by 1 cm^2 could then be calculated, knowing the recorder chart speed. All experimental and test runs were conducted at 15 cm/hr chart speed. The quantity of water loss per hour, at a particular deflection level could be calculated using the following equation:

$$\dot{M} = 15(XC)$$

where,

$\dot{M}$ = Quantity of Water Lost per Unit Time (g/hr)

15 = Chart Speed (cm/hr)

X = Steady-State Pen Deflection (cm)

C = Quantity of Water Represented by 1 cm^2 (g/cm^2).

Knowing the quantity of water lost per hour, the absolute

humidity is determined as :

$$\sigma = (1000M)/\dot{V}_{STPD}$$

where,

σ = Absolute Humidity (kg/m^3)

$\dot{V}_{STPD}$ = Air Flowrate (ml/hr) at Standard Temperature and Pressure.

The percent relative humidity is calculated by:

$$\phi = 100\ (\rho/p_{s,Ta})$$

where,

ϕ = Percent Relative Humidity

ρ = Absolute Humidity (kg/m^3)

$p_{s,Ta}$ = Saturated Water Vapor Density at T_a

T_a = Room Temperature (C).

A calibration curve was produced for both 1 and 2 volt sensitivity settings, with 12 calibration points at 1 volt, covering a range of 22.41%rh to 86.00%rh (Figure A18) and 8 calibration points at 2 volts, over a range of 31.90%rh to 94.70%rh (Figure A19).

Figure A18. Relative humidity calibration - 1 volt. Pen deflection (ordinate: cm; pen) is presented as a function of percent relative humidity (abscissa: %rh) at 1 volt sensitivity. Pen deflection = -6.9919 + (.3284)(%rh) r = .99

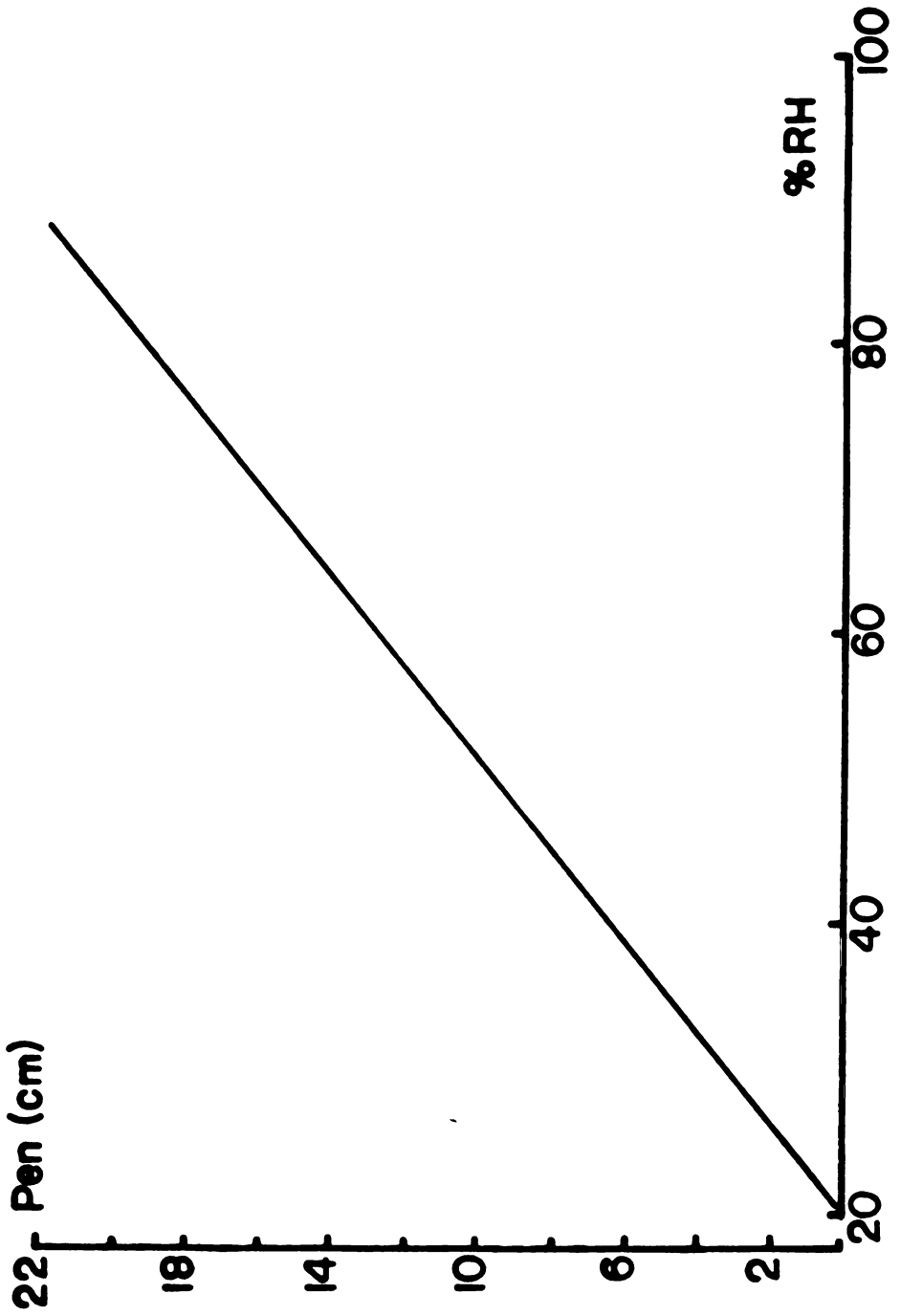


Figure A18

Figure A19. Relative humidity calibration - 2 volt. Pen deflection (ordinate: cm; pen) is presented as a function of percent relative humidity (abscissa: %rh) at 2 volt sensitivity. Pen deflection = -2.6719 + (.1486)(%rh) r = .97

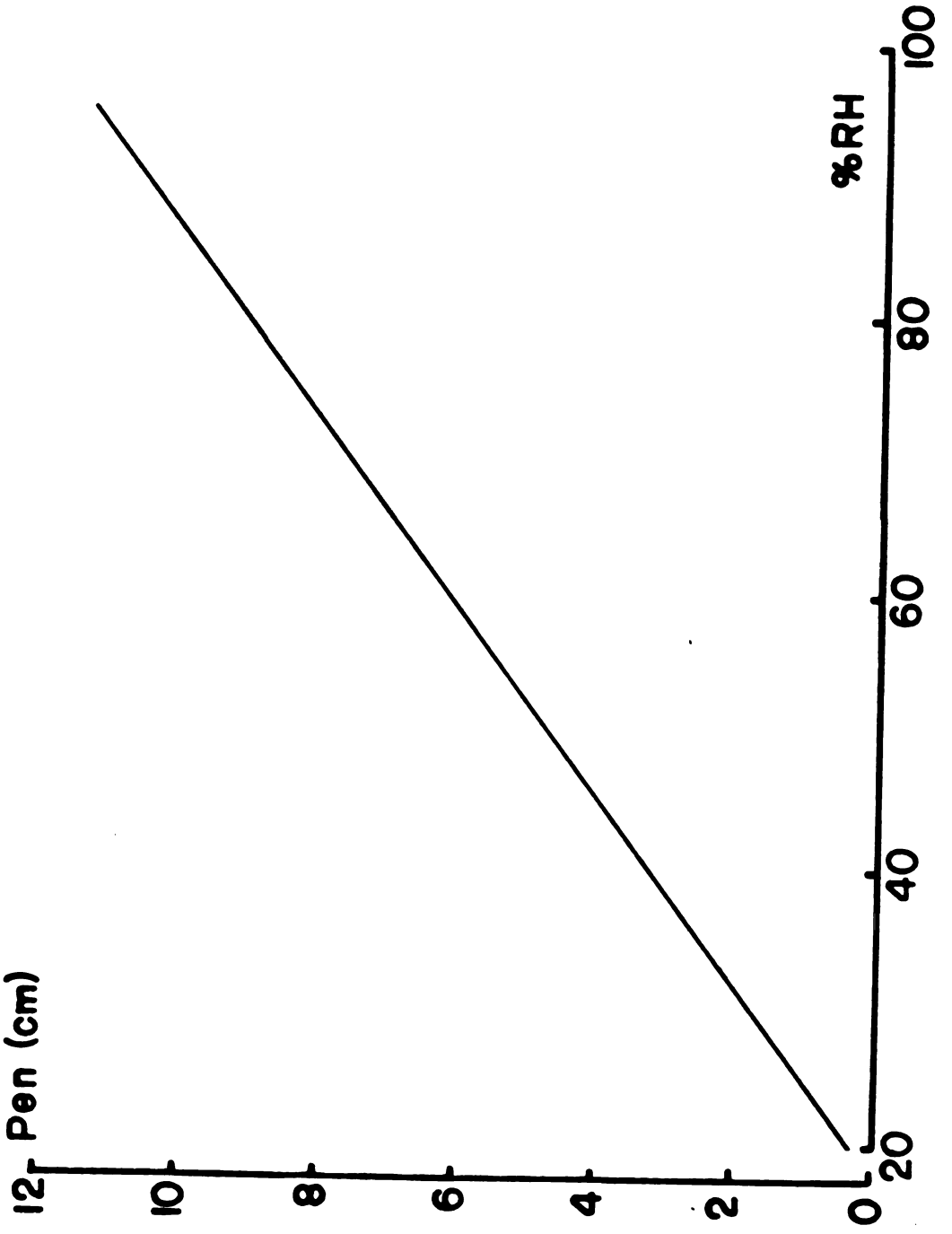


Figure A19

Sample Calculation:

$\dot{V}_{ATP}$	BP	T_a	$p_{s,Ta}$	water loss
294 ml/min	745 mmHg	26.8C	2.5472 x 10^{-2} kg/m^3	.14095 g

area under curve
90.89 cm^2

$\dot{V}_{STPD}$ = 294ml/min + (745mmHg/760mmHg) + [273K/(273K + 26.8C)]

$\dot{V}_{STPD}$ = 262.5 ml/min = 15750 ml/hr

C = (.14095 g/90.89 cm^2) = 1.5508 x 10^{-3} g)

if X = 1,

$\dot{M}$ = 15(1)(1.55 x 10^{-3}g) = 2.326 x 10^{-2}g/hr

σ = [1000(2.326 x 10^{-2}g/hr)/15750 ml/hr] = 1.477 x 10^{-3}kg/m^3

ϕ = [100][(1.477 x 10^{-3}kg/m^3)(2.5472 x 10^{-2}kg/m^3)] = 5.798 %

The steady-state pen deflection was 9 cm, therefore,

ϕ at 9 cm = 52.187 %

This value was then used as a calibration point.

APPENDIX 10

THERMOCOUPLE CONSTRUCTION AND CALIBRATION

APPENDIX 10

THERMOCOUPLE CONSTRUCTION AND CALIBRATION

All thermocouples were constructed of 40-gauge copper-constantan wire (Omega Engineering Inc., Stamford, Conn.). This was accomplished by first removing approximately 2cm of insulation from the ends of both the copper and constantan wires. The bare leads were twisted together and soldered using resin core solder 60/40 (Kester Products, Chicago, Ill.). Then a thin layer of Insl-x (Insl-x Products Corp., Yonkers, N.Y.) was applied to the soldered copper-constantan junction. All thermocouples were calibrated to the nearest .125C using a National Bureau of Standards thermometer (Figure A20).

Figure A20. Thermocouple calibration curve. Pen deflection (ordinate: chart units; pen) is presented as a function of temperature (abscissa: C; T). A straight line was fitted through the points by regression analysis.

Pen deflection = -.839 + (2.0272)(T)

r = .99

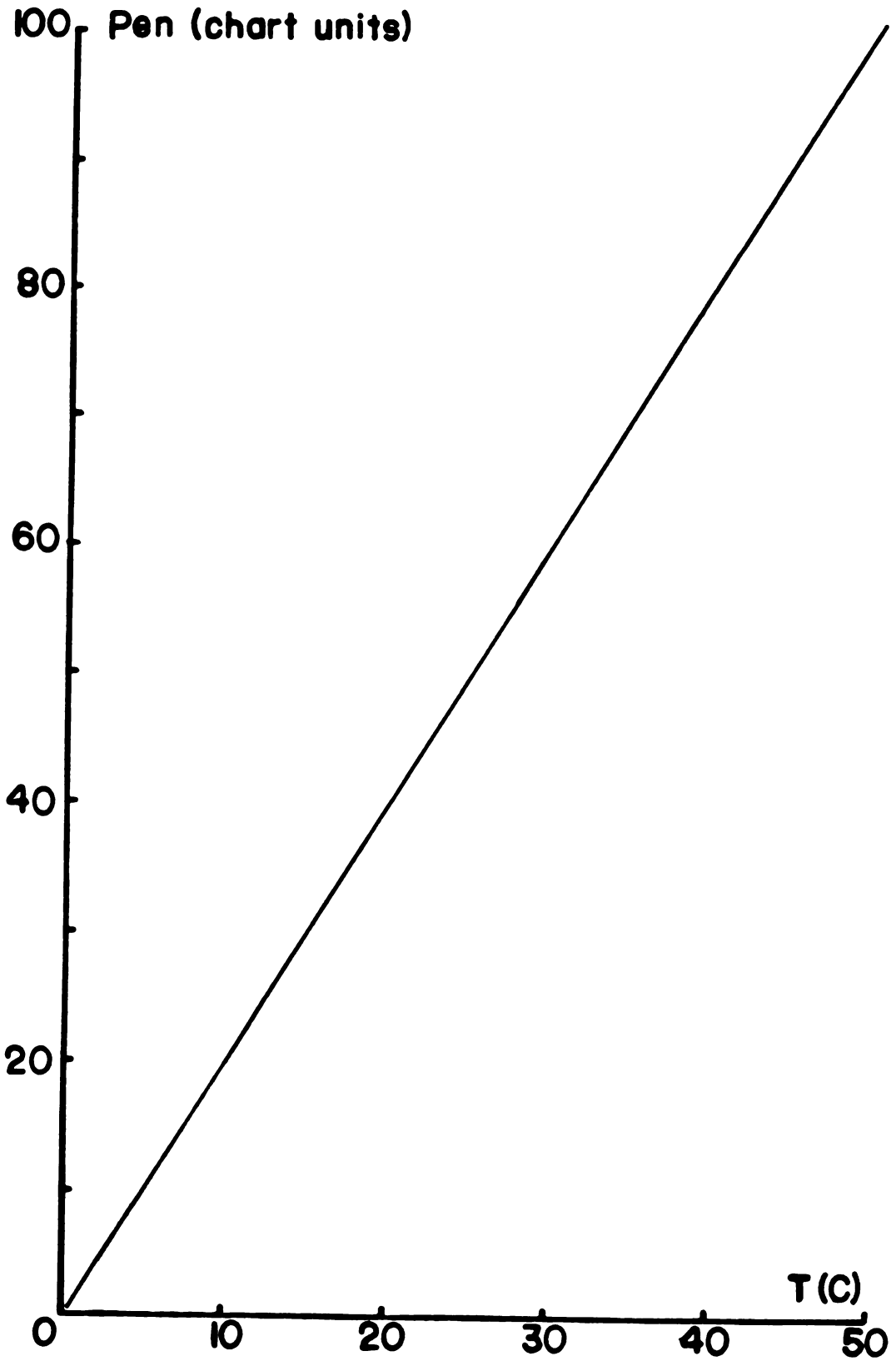


Figure A20

APPENDIX 11

SAMPLE CALCULATIONS OF THERMOREGULATION DATA

APPENDIX 11

SAMPLE CALCULATIONS OF THERMOREGULATION DATA

Data:

$\dot{V}_{I(ATP)}$	T_a	T_b	T_c	Body Weight	BP
560ml/min	25.6C	41.15C	30.0C	191g	746.1mmHg

$F_{E_{O_2}}$	$F_{E_{CO_2}}$	p_{s,T_a}	ϕ
20.34%	0.61%	.023832kg/m^3	24.64%

Calculations:

$$\dot{V}_{I(STPD)} = 560\text{ml/min} \times \frac{746.1\text{mmHg}}{760.0\text{mmHg}} \times \frac{273.0\text{C}}{298.6\text{C}}$$

$$= 502.625\text{ml/min}$$

$$\rho = \frac{(24.64\%)(.02383\text{kg/m}^3)}{100} = 5.872 \times 10^{-3}\ \text{kg/m}^3$$

$$\dot{M} = \frac{(5.872 \times 10^{-3}\text{kg/m}^3)(30157.5\text{ml/hr})}{1000} = .1771\text{g/hr}$$

$$E = \frac{(580\text{cal/g})(.1771\text{g/hr})(1.163 \times 10^{-3}\text{W/cal})}{191\text{g}}$$

$$= 6.254 \times 10^{-4}\text{W/g}$$

$$\dot{V}_{O_2} = \frac{(502.625\text{ml/min})}{(1-.2034-.0061)} \times .005319 = 3.38\text{ml/min}$$

$$\dot{V}_{CO_2} = \frac{(502.625\text{ml/min} - 105.551\text{ml/min})}{.7905} \times .0061$$

$$= 3.06\text{ml/min}$$

$$R = 3.06/3.38 = .905$$

$$M = \frac{(13.084\text{ml/min} + 3.654\text{ml/min})}{191\text{g}} \times 1.163\times10^{-3}$$

$$= 6.116\times10^{-3}\ \text{W/g}$$

$$C = \frac{6.116\times10^{-3}\text{W/g}}{(41.15\text{C} - 30.00\text{C})} = 5.485\times10^{-4}\text{W/g C}$$

$$C_{dry} = \frac{(6.116\times10^{-3}\ \text{W/g} - .6254\times10^{-3}\ \text{W/g})}{(41.15\text{C} - 30.00\text{C})}$$

$$= 4.924\times10^{-4}\text{W/g C}$$

APPENDIX 12

THYROXINE AND TRIIODOTHYRONINE RADIOIMMUNOASSAY

APPENDIX 12

THYROXINE AND TRIIODOTHYRONINE RADIOIMMUNOASSAY

Reference: Immunostat T_4 and T_3 Test Kits for the Quantitation of Thyroxine and Triiodothyronine, Meloy Laboratories, Inc., Biological Products Division, Springfield, Virginia

Principle:

The assay works on the principle that a specific hormone antibody cannot distinguish between the labelled and unlabelled hormone. When ^{125}I-T_3 or ^{125}I-T_4 are mixed with T3 or T_4, respectively, in the presence of the specific hormone antibody, they compete for binding sites on the antibody. The lower the concentration of unlabelled hormone present in the solution, the higher the level of labelled hormone which binds to the antibody.

Thyroxine or triiodothyronine-binding plasma proteins are inhibited from binding the thyroid hormones during the assay. This is mainly accomplished by diluting the samples to such a degree that the binding of T_4 and T_3 to plasma proteins is inhibited. In addition, birds do not have thyroxine binding globulin, which is the major T_3 and T_4 binding protein in man. Also, the levels of plasma albumin

and prealbumin are lower in birds than in mammals. The result is that there is more free T_3 and T_4 in avian than in mammalian plasma and less problems with hormone-protein binding.

Once the labelled and unlabelled hormones are combined with the specific antibody, the mixture is incubated for the required period of time to reach reaction equilibrium. Ammonium sulfate reagent is then added to the mixture to precipitate the antigen-antibody complex. Once the bound labelled and unlabelled hormones have precipitated, the mixture is centrifuged to further separate supernatant and precipitate. The supernatant is then aspirated off and the precipitate counted using a gamma scintillation counter.

Reagents:

a. T_3 radioimmunoassay
   1. Immunostat T_3 standards - 0,25,50,150 and 600ng/dl of liothyronine in T_3-free serum
   2. Immunostat T_3 antiserum, diluted in 13ml of 0.05 molar sodium barbital with 0.1% bovine serum albumin and 0.1% sodium azide
   3. Immunostat T_3 ammonium sulfate precipitating reagent, saturated $(NH_4)_2SO_4$ with 12% normal rabbit serum and 0.1% sodium azide
   4. Immunostat T_3 ^{125}I-T_3 ANS-Buffer, 0.05 molar sodium barbital buffer, 0.1% sodium azide, 0.33 mg/ml of ammonium salt of 8-anilino-1-napthalene

sulfonic acid, ^{125}I labelled triiodothyronine diluted to contain a total of 6uCi of ^{125}I-T3 with 0.01% bovine serum albumin

b. T_4 radioimmunoassay

1. Immunostat T_4 standards - 0.0,1.0,3.0,10.0 and 25.0 µg/dl of thyroxine in T_4-free serum
2. Immunostat T_4 antiserum, diluted in 13ml of 0.05 molar sodium barbital with 0.1% sodium azide
3. Immunostat T_4 ammonium sulfate precipitating reagent, saturated $(NH_4)_2SO_4$ with 15% normal rabbit serum and 0.1% sodium azide
4. Immunostat T_4 ^{125}I-T_4 ANS-Buffer, 0.05 molar sodium barbital buffer, 0.1% sodium azide, 0.19mg/ml of ammonium salt of 8-anilino-1-napthalene sulfonic acid, ^{125}I labelled thyroxine diluted to contain total of 4µCi of ^{125}I-T_4 with 0.01% bovine serum albumin

Procedure:

The T_3 and T_4 radioimmunoassays are very similiar. In the following assay description, emphasis will be placed on points of dissimiliarity between the two procedures. All other steps are identical.

All reagents were stored at 4C and allowed to equilibrate to room temperature for 1 hour before use. Exactly 1.0ml of ^{125}I-T_3 or ^{125}I-T_4 was added to all tubes. Standards and plasma samples were added next in volumes of 100ul for T_3 and 10µl for T_4 analysis. Non-specific binding

tubes received the appropriate volume of Ø standard for both the T_3 and T_4 analysis. 100ul of either T_3 or T_4 antiserum was added to all tubes except non-specific binding tubes, which received 100µl of deionized water. All tubes were immediately vortexed and allowed to incubate at room temperature for 60-120 minutes for T_3 analysis and 20-120 minutes for T_4 analysis. During the incubation period, several tubes were counted for the length of time required to obtain 10,000 counts and the time recorded. These counts were used later for data analysis. Once the tubes had incubated for the required length of time, 1.0ml of ammonium sulfate was added to each tube. All tubes were vortexed again and centrifuged at 2600 RPM for 15 minutes. After centrifugation, the supernatant was aspirated off using a vacuum line connected to an erylemeyer flask reservoir. The pellet and test tube were then placed in the counting well of the scintillation analyzer/scaler and counted for the length of time required to obtain 10,000 counts.

Calculations:

The average counts per minute for each sample was converted to a percent bound/total ratio (%B/T ratio) by using the following equation:

$$\%B/T = [(B - NSB)/(TC - NSB)] \times 100$$

where,

%B/T = percent bound/total

B = sample counts per minute

NSB = non-specific binding counts per minute

TC = total counts per minute

The standard curve was obtained by plotting the %B/T ratio for each standard on the ordinate (arithmetic scale) and the T_3 or T_4 concentration on the abscissa (log scale). A straight line was fitted through the points by linear regression analysis and the linear equation was used to calculate the hormone level.

Sample Calculation:

Tube	Counts/minute	%B/T
Total Counts	19802	-----
NSB	2389	-----
25ng% Standard	9759	42.33
50ng% Standard	8824	36.95
150ng% Standard	5780	19.47
600ng% Standard	3920	8.79
Unknown	6811	25.39

$$Y = 85.0952 + (-29.665)(\log X)$$

where,

Y = %B/T

X = T_3 concentration (ng/dl)

$$25.39 = 85.0952 + (-29.665)(\log X)$$

$$X = 102.95 \text{ ng\%}$$

Assay Performance:

a. Intra-Assay Variance

Duplicate blood samples were collected from seven adult bobwhite and mean T_3 values were determined for each bird with ± 1 standard error. Means and standard errors were averaged together too determine the overall mean value which was 289.66 $\pm$25.43ng%. Seven birds were also tested for plasma T_4 levels, using multiple plasma samples from each bird. The mean T_4 level was 1.69 $\pm$.139µg%. In both cases, there was a standard error of approximately $\pm$8.5% around the mean values. This indicates that both T_3 and T_4 radioimmunoassays are repeatable.

b. Recovery Determination

A test was conducted to determine if the avian plasma proteins interferred with the ability of the radioimmunoassay to detect free thyroid hormones. A known quantity of T_4 or T3 was added to an avian plasma sample and then tested to determine the percentage of added hormone which was detectable in the mixture. Six T_4 and nine T_3 recovery analyses were conducted and yielded mean recoveries of 109.9$\pm$5.48%T_4 and 108.8$\pm$8.7%T_3. This shows that the avian plasma proteins do not interfer with the ability of the radioimmunoassay to detect free thyroid hormones.

c. Radioimmunoassay Specificity

Meloy Laboratories determined the crossreactivity of the T3 and T_4 antiserums with other iodinated amino acid analogs by measuring the amount of each analog required to displace 50% of labelled T_3 or T_4 from the antibody (Table A2, A3).

Table A2. Triiodothyronine specificity

	Concentration Required for 50% Displacement (ng%)	Percent Cross Reactivity by Weight
L-Triiodothyronine	180	1.0
3,3,5 Triiodo Thyro Acetic Acid	300	0.6
3,5 D,L-Thyronine	40,000	0.0045
3,5 Diiodo-L-Thyronine	78,000	0.0023
L-Thyroxine (T_4)	100,000	0.0018
D-Thyroxine	>300,000	<0.0006
3 Iodo-L-Tyrosine (MIT)	>300,000	<0.0006
3,5 Diiodo-L-Tyrosine (DIT)	>300,000	<0.0006
L-Thyronine	>300,000	<0.0006
D,L-Thyronine	>300,000	<0.0006

Table A3. Thyroxine specificity

	Concentration Required for 50% Displacement (ng%)	Percent Cross Reactivity by Weight
L-Thyroxine (T_4)	5.0	1.000
D-Thyroxine	6.7	0.746
L-Triiodothyronine (T_3)	155.0	0.033
3,3,5 Triiodo Thyro Acetic Acid	340.0	0.015
3,3,5 Triiodo-L-Thyronine	540.0	0.009
3 Iodo-L-Tyrosine (MIT)	>300.0	<0.016
3,5 Diiodo-L-Tyrosine (DIT)	>300.0	<0.016
L-Thyronine	>300.0	<0.016
D,L-Thyronine	>300.0	<0.016
3,5 D,L-Thyronine	>300.0	<0.016
3,5 Diiodo-L-Thyronine	>300.0	<0.016

The cross reactivity of other iodinated amino acid analogs with either the T_3 or T_4 antiserum is minimal.

APPENDIX 13

GAMMA RADIATION COUNTING AND ANALYSIS

APPENDIX 13

GAMMA RADIATION COUNTING AND ANALYSIS

Reference: Operator's Manual, Model 8725 and 8727 Analyzer/Scaler, Nuclear Chicago, Des Plaines, Ill.

Principle:

Electromagnetic rays are emitted by the gamma emitting ^{125}I isotope and are detected by gamma-sensitive scintillation detectors. The detector is composed of a thallium-activated, sodium iodine crystal and a photomultiplier tube. Gamma particles, which enter the crystal, react with the electrons of the crystal. These gamma reactions produce "flashes of light" or scintillations within the crystal. The magnitude of the scintillations is proportional to the amount of energy released by the gamma reaction. A photomultiplier tube detects the scintillations and emits an output pulse with a magnitude that is proportional to the energy released by the gamma events. The detector sends the pulses to the analyzer where they are amplified and a selection is made between desired and undesired pulses.

Calibration:

Upper and lower level discriminators were adjusted to set the appropriate window width for ^{125}I. Any backgroud radiation which possessed energies higher or lower than the discriminator levels would automatically be rejected and decrease background radiation detected by the analyzer. In addition, any remaining background radiation was automatically subtracted by the analyzer from the sample activity.

A ^{137}cesium reference was obtained from the Radiation Safety Laboratory at Michigan State University. The analyzer was set at the Ø to 1 Mev energy range and the reference source utilized to center the principle photopeak for ^{137}cesium in a 10% counting window. The window was then repositioned, after removing the reference source, to the photopeak energy level for ^{125}I (Ø.Ø35 Mev) by adjusting the base control setting. The control settings for ^{125}I were checked with the setting values provided by Dr. E. P. Reineke for the specific analyzer and found to be identical.

APPENDIX 14

BIOLOGICAL HALF-LIFE DETERMINATION

APPENDIX 14

BIOLOGICAL HALF-LIFE DETERMINATION

Reference: Etta, 1968

Principle:

The utilization and breakdown of a particular hormone can be determined by measuring the rate at which a quantity of the labelled hormone is removed from the blood. Recycling of the radioactive label must be inhibited during the test, to avoid underestimating the biological half-life of the hormone.

Reagents:

1. L-(^{125}I)thyroxine (New England Nuclear Laboratories, Boston, Mass.) 116.40µCi/µgT_4, 2.00µg T_4/ml in a 1:1 solution of n-propanol:water
2. L-3,5,3-(^{125}I)triiodothyronine (New England Nuclear Laboratories, Boston, Mass.) 111.16µCi/ug T_3, 2.14µgT3/ml in a 1:1 solution of n-propanol:water
3. sodium thiocyanate solution, 40mg/ml diluted in 0.9% physiological saline (Mallinckrodt Chemical Works, St. Louis, Missouri)

Procedure:

The biological half-lives of T_3 and T_4 were measured by injecting ^{125}I-T_3 and ^{125}I-T_4 into the adult and immature quail (21 and 42 day old) and recording the decrease in plasma radioactivity as a function of time. Two concentrations of T_3 and T_4 were produced for injection into the birds and are presented in Table A4.

Table A4. Concentration of injectants

Age (days)	T_4 (µg/bird)	T_3 (µg/bird)
21	.01	.01
42	.05	.02
Adult	.05	.02

These hormone concentrations provided a suitable level for injection which would not exceed the total concentration of T3 or T_4 normally found in each age of quail tested. Quail plasma was mixed in each solution to decrease the amount of ^{125}I absorption by the glassware. All solutions were diluted using 0.9% physiological saline (Table A5).

Table A5. Composition of injectants

Thyroid Hormone Concentration	Composition		
	^{125}I-Thyroid Hormone (ml)	Quail Plasma (ml)	Saline (ml)
T_4 (.1ug/ml)	0.10	0.10	1.80
T_4 (.5ug/ml)	1.00	0.20	2.80
T_3 (.1ug/ml)	0.20	0.20	3.60
T_3 (.2ug/ml)	0.30	0.16	2.74

Recycling of ^{125}I was prevented by injecting sodium thiocyanide, which inhibits the uptake of iodide by the thyroid. The solution was injected subcutaneously into the quail at the start of the experiment. The dosage of sodium thiocyanate injected into the adult quail was identical to that used by Etta (1968), with the younger quail receiving the same proportion of sodium thiocyanate to body weight as the adults. The dosages were 20mg/bird, 10mg/bird and 4mg/bird for the adult, 42 and 21 day old, respectively. One hour after the injection of sodium thiocyanate, ^{125}I-T_3 or ^{125}I-T_4 was injected into a brachial vein. Blood was removed from a brachial vein or by cardiac puncture at 3 hour intervals over a 12 hour period following the injection of the labelled hormone. A sufficient quantity of blood was removed to provide a minimum plasma volume of 50µl.

All blood samples were heparinized and spun in an IEC MB Micro Hematocrit Centrifuge. A 50 or 100µl plasma sample

was withdrawn and activity measured by the Model 8725 Nuclear Chicago Scintillation Counter (Nuclear Chicago Corp., Des Plaines, Ill.). Each sample was counted for the length of time required to obtain 10,000 counts. Background counts were automatically subtracted from the total counts during the counting process.

Calculations:

Each sample was normalized by calculating the percentage of the injected dose in that sample.

$$\text{Percentage Injected Dose} = \frac{\text{Sample Count/Unit Volume}}{\text{Injectant Count/Unit Volume}}$$

The percentage injected dose was plotted on a logarithmic scale (ordinate) as a function of time on the arithmetic scale (abscissa). A regression line was fitted through the points by linear regression analysis. The T_3 and T_4 half-life was calculated by using the following equation:

$$t\ 1/2 = .693/(2.3b)$$

where,

$t\ 1/2$ = hormone half-life

b = slope of the regression line

2.3 = constant required for the transformation of $\log_{10}$ to natural logarithms

APPENDIX 15

ALBUMIN COLORIMETRIC DETERMINATION BY BROMCRESOL GREEN METHOD

APPENDIX 15

ALBUMIN COLORIMETRIC DETERMINATION BY BROMCRESOL GREEN METHOD

Reference: Tietz, 1976

Principle:

Albumin reacts with a large number of chemicals by electronic and tertiary van der Waal's forces and by hydrogen bounding. There are many anionic colored dyes (i.e. bromcresol green) which react with albumin in this way. The binding of these dyes must not be affected by changes in hydrogen ion concentration or ionic strength. In addition, the color of the albumin-bound dye should be different from the color of the unbound dye and blood pigments. Bromcresol green fulfills these requirements and is suitable for the albumin colorimetric determination.

Reagents:

Bromcresol Green Solution (Sigma #630, Sigma Chemical Co., St. Louis, Missouri)

Protein Standard Solution, 5.0% albumin (Sigma #540-10, Sigma Chemical Co., St. Louis, Missouri)

Procedure:

Bromcresol green solution (3.0 ml) was pipetted into standard and unknown tubes. A 5.0g% albumin standard solution was diluted in 0.9% physiological saline to produce albumin standards of .2, .625, 1.25, 2.5g% albumin. Standard and unknown solutions (50ul) were added to the bromcresol green, vortexed, and allowed to incubate at room temperature for 10 minutes.

A Coleman Model 139 Perkin-Elmer UV-VIS Spectrophotometer (Figure A21) was set at 630nm (Tietz, 1976) for reading absorbances of standards and unknowns. The spectrophotometer was set at 100% transmittance using first a water blank and then the reagent blank. Zero % transmittance was set by closing the emitter light shutter and adjusting zero control to achieve 0% transmittance. Each standard and unknown was inserted separately into the spectrophotometer and its absorbance read to the nearest $\pm$.01 unit.

Figure A21. Albumin standard curve. Absorbance (ordinate: Y) is presented as a function of albumin concentrations (abscissa: X; g%) for .2, .625, 1.25, 2.50g% albumin standards.

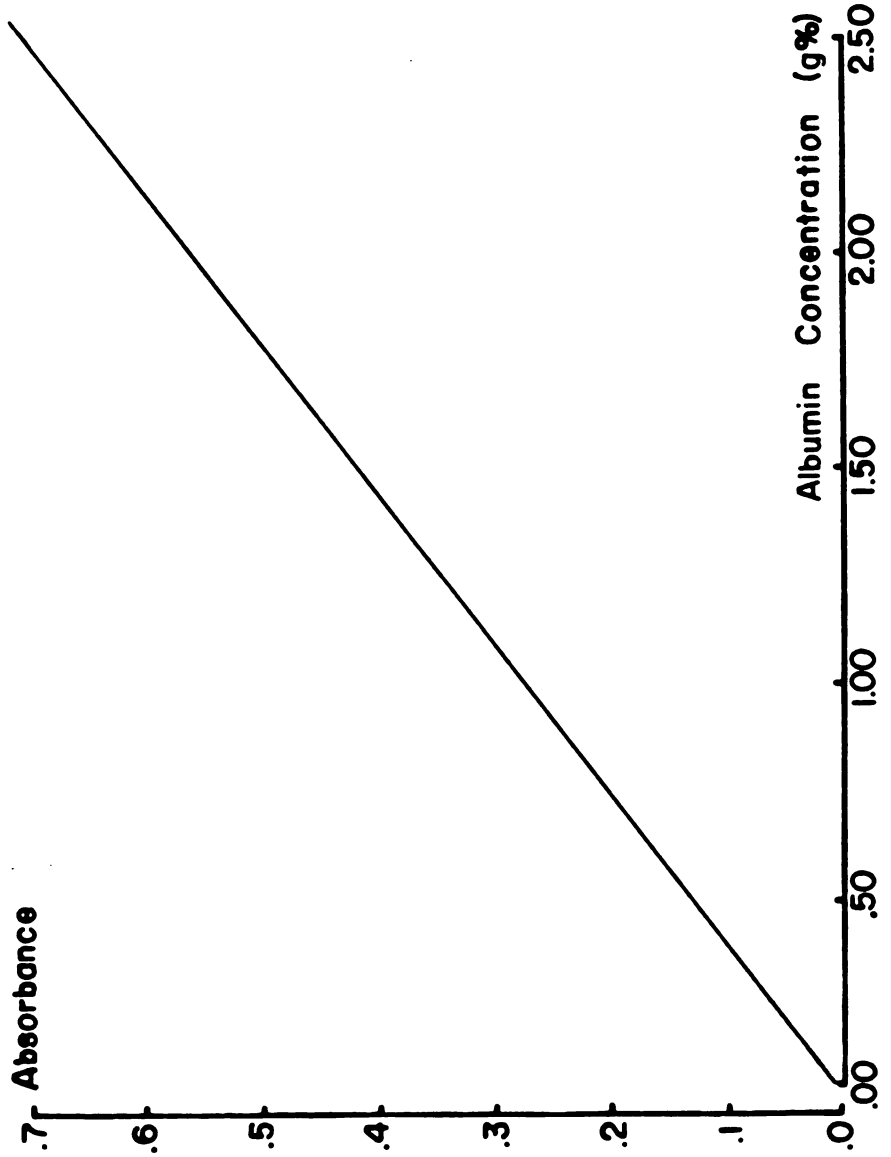

Absorbance
.7
.6
.5
.4
.3
.2
.1
0
.00
.50
1.00
1.50
2.00
2.50
Albumin Concentration (g%)

Figure A21

Calculations:

A straight line was fitted through a plot of standard values versus absorbances by linear regression analysis. Unknown concentrations were determined by using absorbance values in the following linear equation:

$$Y = -.01615 + (.29434)(X)$$

where,

Y = absorbance

X = albumin concentration (g%)

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