

GROWTH AND ENERGY REQUIREMENTS
OF CAPTIVE
GREAT BLUE HERONS (ARDEA HERODIAS)
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ABSTRACT

The energy requirements of Great Blue Herons (*Ardea herodias*) during critical stages of their life-history when food is considered limiting were investigated.

The metabolizable energy coefficients (MEC) of herring (*Clupea harengus*), mackerel (*Scomber scombrus*) and trout (*Oncorhynchus mykiss*) when fed to Great Blue Herons were determined. Estimates of apparent MEC of mackerel and trout were affected by the level of energy intake. Correcting for endogenous energy losses in the excreta yielded estimates of true MEC that were independent of energy intake. True MEC of mackerel and trout averaged 0.866 ± 0.014 . Correcting for nitrogen retention did not improve the estimates of MEC. Estimates of MEC of herring were highly variable, possibly due to rancidity of the herring.

A continuous feeding trial was used to determine the energy requirements of 12 hand-reared Great Blue Heron chicks. Male (n=8) and female (n=4) chicks did not differ in their hatching mass, but, by day 30 the mass of male chicks was significantly greater than the mass of female chicks. Male chicks were about 13% heavier than female chicks at fledging. Metabolizable energy intake (EI_{ME}) and energy requirements did not differ between male and female chicks. EI_{ME} was maximum between days 26 and 41 at 2027 ± 25 kJ/d. Total energy required for maintenance (kJ/d) was greatest between 30 and 39 d of age. Total energy required for gain (kJ/d) was greatest

between 10 and 29 d of age, the time of maximum growth.

The maintenance energy requirements (E_{MAIN}) of captive male Great Blue Herons were determined by a continuous feeding trial through two autumn and winter periods (year 1, $n = 4$; year 2, $n = 10$) that differed in the severity of their winter months. Body mass increased through the autumn to a maximum in early winter and declined during late winter. Herons gained about 650 g between August and the time of peak winter mass. This reserve could potentially meet a heron's total maintenance energy requirements for about 6 d. The lower critical temperature for energy intake and E_{MAIN} were 7.9°C and 7.6°C , respectively.

The findings in this thesis provide evidence to support field observations that indicate the importance of food limitations as determinants of life-history traits in herons.

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Chapter 1
General Introduction

All living organisms must obtain and convert energy from the environment to maintain themselves, grow and reproduce. The amount of energy that an animal must procure and allocate to these various activities depends upon an interplay of many abiotic and biotic factors (King 1974; Ricklefs 1974; Walsberg 1983). Animals need a constant input of energy to maintain life (ie. to maintain structure and function). This is referred to as existence or maintenance energy requirements (E_{MAIN}). All energy intake above that required for maintenance can be either stored for future use or invested in production, such as growth and reproduction.

Energy partitioning

Animals derive all of their energy from the food that they eat, but not all of this energy is available for maintenance and production. The degree with which dietary energy is available may vary from 0 to 100 % depending on the completeness of digestion and oxidation of the ingested energy. A generalized scheme describing energy utilization by animals is presented in Figure 1.1. Details of each partition are described below (summarized from Harris 1966; Kendeigh et al. 1977; Sibbald 1982).

Gross energy (GE) is the energy contained in the food that is eaten by the animal. It is measured as the quantity of heat resulting from the complete oxidation of the food by bomb calorimetry. The gross energy content of food varies in relation to its nutrient composition. Lipid (39.5 kJ/g) has

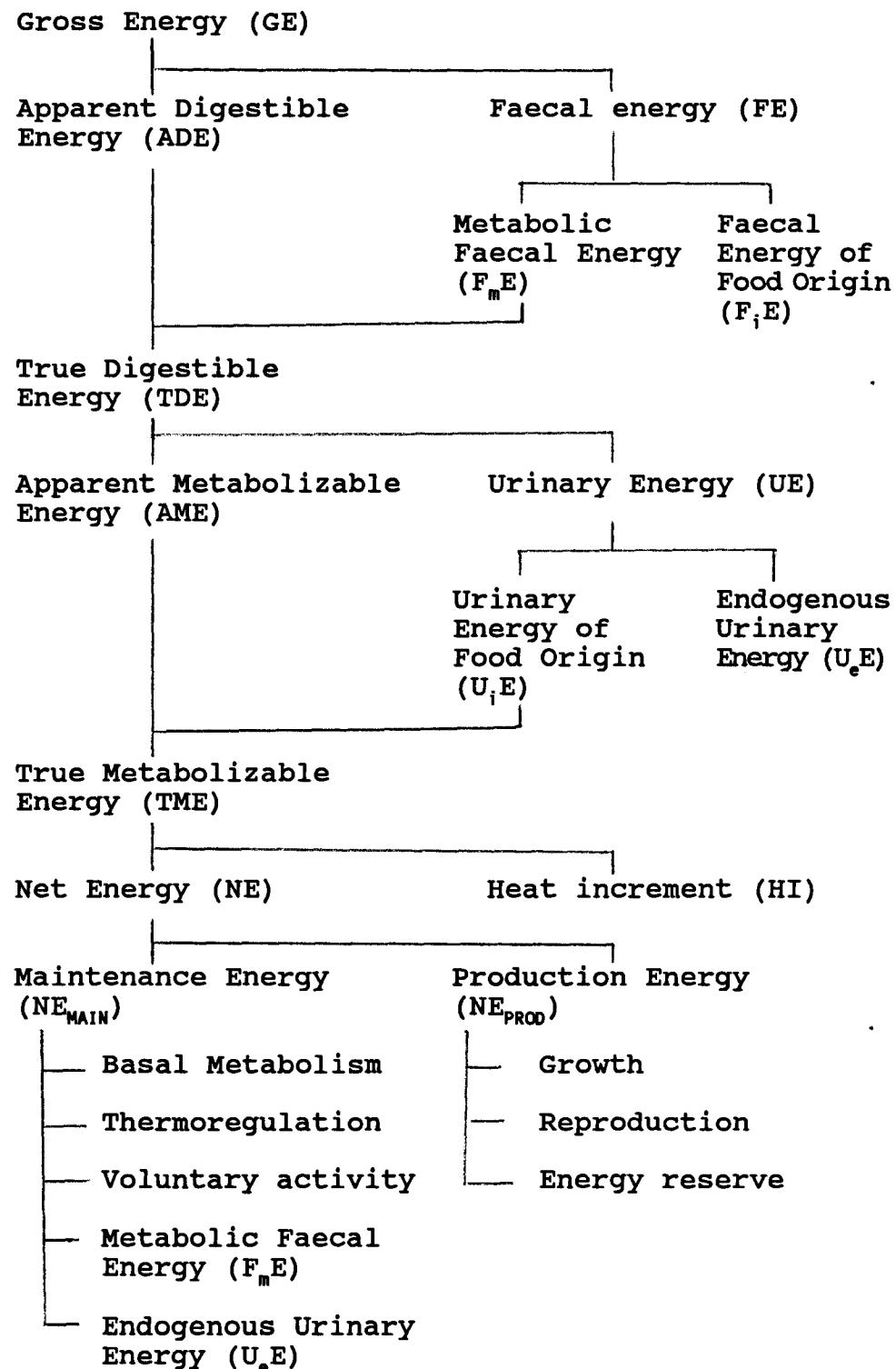


Fig. 1.1. A generalized scheme describing the partitioning of ingested energy by animals (adapted from Harris 1966; Kendeigh et al. 1977; Sibbald 1982).

approximately twice the energy value of carbohydrate (17.3 kJ/g) or protein (23.6 kJ/g).

Digestible energy is the difference between the ingested GE and the energy voided in faeces (FE). It is generally measured as apparent digestible energy (ADE) because not all FE is of feed origin (ie. faecal energy of food origin; F_iE). FE also contains a metabolic fraction (F_mE) comprised of unabsorbed digestive secretions and sloughed intestinal mucosal cells. Gaseous products of digestion (GPD) are the combustible gases produced by microflora in the gastrointestinal tract. Correcting for F_mE and GPD yields true digestible energy (TDE), which is the amount of energy absorbed from the gastrointestinal tract [ie. $TDE = GE - (F_iE + GPD)$, where $F_iE = FE - F_mE$].

Not all TDE is available to the animal, as a portion of the absorbed energy is voided in the urine without having been utilized by the animal. Apparent metabolizable energy (AME) is the difference between TDE and the energy voided in the urine (UE). It is termed 'apparent' because not all UE is of food origin (ie. urinary energy of food origin; U_iE). UE also contains an endogenous fraction (U_eE) comprised of products of tissue catabolism. Correcting for U_eE yields true metabolizable energy, which is the amount of energy retained in the body from the diet [ie. $TME = GE - (F_iE + GPD + U_iE)$, where $F_iE = FE - F_mE$ and $U_iE = UE - U_eE$].

Animals have higher rates of metabolism while digesting

and assimilating food. This increased heat production is termed heat increment of feeding (HI). For animals within their thermoneutral zone, HI is simply lost from the body as waste heat. For animals below their thermoneutral zone, HI may contribute to the maintenance of body temperature.

Net energy (NE) is the difference between TME and HI and represents the amount of energy available for maintenance and production. Net energy for maintenance (NE_{MAIN}) is used for basal metabolism, voluntary activity, thermoregulation, metabolic faecal energy and endogenous urinary energy. Net energy for production (NE_{PROD}) is used for work, tissue gain (growth, energy reserves, feathers, etc.) or reproduction (eggs, semen, etc.)

Energy budgets

Energy budgets compartmentalize the energy flow through an animal. From the energy partitioning scheme of Figure 1.1 a simple energy budget can be constructed for an animal as follows:

$$\begin{aligned} NE &= GE - [(FE - F_m E) + GPD + (UE - U_e E) + HI] \\ &= NE_{MAIN} + NE_{PROD}. \end{aligned} \quad (1.1)$$

This energy budget can be further simplified to:

$$\begin{aligned} ME &= GE - [(FE - F_m E) + (UE - U_e E)] \\ &= ME_{MAIN} + ME_{PROD} \end{aligned} \quad (1.2)$$

where ME_{MAIN} and ME_{PROD} are the metabolizable energy requirements for maintenance and production, respectively. This simplification is valid because 1) energy losses due to GPD

are small in non-herbivores and 2) HI may be considered part of ME_{MAIN} if used to keep the body warm. Generally, energy budgets for birds are constructed by examining the partitioning of ME into the energy requirements for maintenance and production.

Several methods have been used to estimate energy requirements (Westerterp 1973; Blehm 1975; Dunn 1975a,b, 1980; Kendeigh et al. 1977; Hurwitz et al. 1978; Ricklefs et al. 1980; Ricklefs and White 1981; Monteverchi et al. 1984; Williams and Print 1986; Roby 1991; Weathers and Sullivan 1991; and others). A combination of the following measurements are usually included: 1) food consumption and excreta production, 2) oxygen consumption, 3) carbon dioxide production and 4) body mass and composition.

It is often difficult make these measurements directly on free-living individuals. Therefore, many studies measure the energy requirements of captive animals and then extrapolate these results to estimate the requirements of free-living animals. Studies with captive animals reflect the energy budget of free-living animals only to the degree in which the captive environment reflects the natural environment. Therefore, the conditions under which the measurements were taken (ie. captive versus free-living, temperature, level of activity, etc.) must be stated in order to fully evaluate the usefulness of this energy budget for free-living animals.

In this thesis, calculations of energy requirements of

captive birds were based on the methods of Sibbald (1976) and Hurwitz et al. (1978). The efficiency with which birds metabolize energy from the diet was determined by the regression method of Sibbald (1976) (see Chapter 2 for methodology) and is expressed as the metabolizable energy coefficient (Kendeigh et al. 1977). Based on a modification of equation 1.2, the energy requirements for maintenance and production (body mass gain) were determined using the method of Hurwitz et al. (1978) (see Chapter 3 for complete methodology). These methods were chosen because they 1) estimate the total energy metabolized by a bird, 2) show the allocation of energy between the requirements for maintenance and production, and 3) do not rely on the sacrifice of animals.

Energy limitations

Energy limitations are important determinants of life-history traits in birds (Martin 1987). The two major periods when energy is thought to be limiting occur during the breeding season and during the winter.

Breeding season. The availability of energy can limit the reproductive success of an animal, as they must meet their maintenance energy requirements before investing in production. Experimental and correlative evidence has shown that food availability affects timing of breeding, clutch size, nestling growth rate, brood size and mass of fledglings (reviewed by Martin 1987).

Natural selection favours individuals that reproduce at a rate above their replacement. Therefore, there exists a trade-off between the amount of energy that parents devote to their own survival and that invested in reproduction. Therefore, parents must decide how much energy to allocate to reproduction and thereby determine the number and quality of young they will try to produce (Martin 1987). Assessment of the energy needs of chicks is therefore important in understanding how much energy parents have to devote to reproduction.

Two strategies of developmental patterns occur in birds; altricial and precocial. These two strategies differ in the allocation of parental care that is invested in the young. Altricial species invest less energy into their eggs and relatively more into parental care, whereas precocial species do the opposite.

Winter. Food limitation outside the breeding season is of major importance because of its effect on survivorship and body condition (Martin 1987). Body mass of many species of birds increases during the winter (Dugan et al. 1981; Ankney 1982; Reinecke et al. 1982; Coulson et al. 1983; Lehikoinen 1987; Ely and Raveling 1989; Rodgers and Rodgers 1990) reflecting increases in lipid and protein stores (endogenous reserves) (King 1972; Reinecke et al. 1982; Ely and Raveling 1989). These endogenous reserves are thought to supply an emergency energy reserve during periods of food shortage or

severe weather (see above references). Body mass of wintering birds has been shown to be positively correlated to survival (Coulson et al. 1983; Haramis et al. 1986).

Post-natal development

Birds exhibit sigmoidal determinate growth. Growth rate is initially low, but increases up to an inflection point, where it begins to decline, causing the accumulation of mass to plateau. Consequently, avian growth data is usually fitted to a sigmoid equation, such as the logistic, Gompertz or von Bertalanffy equations. These three equations differ principally in the timing of their inflection point (time of maximum growth rate).

Ricklefs (1968, 1973, 1979) examined growth rates among various species of birds and found that a large proportion of the variation in growth rates was related to adult body mass (asymptote of growth curves). The relationship between chick growth rates (k) and adult body mass (asymptote, A) is described by the following allometric equation:

$$k = 1.10 A^{-0.34} \quad (1.3)$$

(Ricklefs 1979). Among birds of similar size, growth rate is related to the precocity of development, with altricial species growing three to four times more rapidly than precocial species (Ricklefs 1973, 1979).

The study species - Great Blue Heron

The life history of Great Blue Herons (*Ardea herodias*) is well documented (Palmer 1962; Hancock and Kushlan 1984; Butler

1991a, 1992).

Diet. Great Blue Herons forage mainly in aquatic habitats, but are also known to forage on grasslands (Butler 1992). Their diet consists predominantly of fish, but they also feed on invertebrates, amphibians, reptiles, birds and mammals (Palmer 1962; Kushlan 1978; Verbeek and Butler 1989; Butler 1992).

Little is known of the energy requirements of Great Blue Herons. Butler (1991b) estimated the daily metabolizable energy intake (assuming a metabolizable energy coefficient of 0.77) of adult herons during four breeding stages to be: egg laying 1163 ± 555 kJ, incubation 1197 ± 194 , feeding small chicks 4264 ± 764 kJ and feeding large chicks 1598 ± 151 kJ.

Breeding. Great Blue Herons nest mostly in colonies located throughout North and Central America. Breeding season varies geographically (Butler 1992). In coastal British Columbia, herons begin to return to colonies in mid January, courtship occurs mid February to early April, and egg laying begins during the first week in April.

Female herons lay eggs at approximately 2 d intervals (Vermeer 1969; Pratt 1970; McAloney 1973) with complete clutch size varying from two to seven eggs (Hancock and Kushlan 1984; Butler 1992). In coastal British Columbia, clutch size averages about four eggs (Butler 1989). Both parents incubate the eggs, beginning shortly after the first egg is laid (Pratt 1970). Incubation period is about 27 d (Vermeer 1969; Pratt

1970; McAloney 1973). Eggs hatch asynchronously, over a period of 2 to 8 d (Butler 1992). Chicks are semi-altricial.

Asynchronous hatching results in the establishment of a size hierarchy among siblings (Quinney 1982; Mock 1985, 1987). The largest chicks get most of the food (Mock 1985, 1987), which consists predominantly of small fish (Simpson 1984; Butler 1991b). As a result, younger chicks grow slower and usually die of starvation (Quinney 1982). Brood size is limited by the ability of parents to gather food (Powell 1983; Sullivan 1988). Chicks fledge in late June or July, between 64 and 91 d of age. In coastal British Columbia, 2.5 chicks are fledged per successful nest (Forbes et al. 1985; Butler 1989).

Non-breeding season. Food limitations occur outside the breeding season. In late autumn, juvenile and adult female herons in coastal British Columbia move from beaches into adjacent grasslands and estuarine marshes because high tides and declining fish populations make foraging unprofitable (Butler 1991b). Starvation is a common cause of mortality of herons (Butler 1991b), particularly during severe winters (Blus and Henny 1981). Juvenile herons have higher rates of mortality than adult herons (Henny 1972; Butler 1991b), presumably because they are less efficient foragers than adult herons (Quinney and Smith 1980; Butler 1991b). Little is known about body mass dynamics of wintering herons.

Survivorship. Henny (1972) calculated a mortality schedule

for Great Blue Herons based upon band recovery data across North American: first year 69.0%, second year 36.3%, subsequent years 21.9%.

Contaminants. The initial impetus for the research in this study was the association of dioxins with reproductive failure of Great Blue Herons nesting in colonies on the Strait of Georgia, British Columbia (Elliott et al. 1988, 1989). Dioxin contamination was shown to be associated with elevated hepatic mixed-function oxidases (Bellward et al. 1990) and reduced growth and development of embryos (Hart et al. 1991). Although the research carried out in this thesis was not concerned with dioxin contamination, it was conducted as a prelude into the effects of dioxins on post-natal growth of Great Blue Herons.

Objectives of thesis research

Little is known of the energy requirements of Great Blue Herons, although many studies have shown that the availability of food affects the location of colonies (Gibbs 1991), timing of breeding (Butler 1991b), reproductive success (Powell 1983; Sullivan 1988) and habitat selection (Butler 1991b). Therefore, the objectives of the research conducted for this thesis were:

- 1) To measure the amount of energy metabolized by Great Blue Herons from fish diets (Chapter 2).
- 2) To describe growth and estimate the energy requirements of Great Blue Heron chicks (Chapter

3).

- 3) To estimate the maintenance energy requirement of Great Blue Herons in relation to environmental temperature (Chapter 4).

CHAPTER 2

**METABOLIZABLE ENERGY OF FISH WHEN FED TO
CAPTIVE GREAT BLUE HERONS (*ARDEA HERODIAS*)¹**

¹Submitted to Canadian Journal of Zoology

Introduction

The ability to estimate how an animal extracts and utilizes energy in its food is important in the assessment of its energy requirements. The amount of available energy in the diet of birds is measured as metabolizable energy (ME; kJ/g), which can be expressed as either apparent (AME) or true (TME) metabolizable energy (Harris 1966; Vohra 1972). AME is the difference between the ingested energy and the amount of energy lost in the excreta. TME corrects for metabolic faecal (F_m) and endogenous urinary (U_e) energy losses in the excreta (Harris 1966; Sibbald 1982). Estimates of ME may be affected both by the level of energy intake and the amount of retained nitrogen (RN) (Wolynetz and Sibbald 1984, Sibbald and Wolynetz 1985).

The efficiency with which an animal utilizes gross energy of the diet has been described as either assimilation efficiency (Castro et al. 1989) or the metabolizable energy coefficient (MEC) (Kendeigh et al. 1977). MEC has been estimated using AME (apparent MEC or AMEC) and not TME (true MEC or TMEC) since AME has been the traditional measure of ME (Miller and Reinecke 1984). MEC can be corrected to zero nitrogen retention as with ME measures.

The objective of the present study was to measure the MEC of fish diets fed to captive Great Blue Herons (*Ardea herodias*). Information obtained from this study was critical in formulating an energy budget for herons (Chapter 3). The

effects of energy intake on estimates of MEC calculated at the level of AME and TME, and their nitrogen corrected equivalents, were also examined.

Materials and Methods

Feeding trials were conducted on 11 captive Great Blue Herons raised from eggs. Herons were housed in an outdoor aviary when not involved in feeding trials and, 0-2 times per day, were hand-fed the same fish used in the feeding trials. Water was provided *ad libitum*.

Herring (*Clupea harengus*), mackerel (*Scomber scombrus*) and gutted and ungutted farmed rainbow trout (*Oncorhynchus mykiss*) were used in feeding trials. The fish were stored at -20°C and thawed overnight prior to feeding. Herons were fed the test fish for at least 4 d prior to experimentation.

During feeding trials, individual herons were housed in crates (37 x 53 x 90 cm) constructed with galvanized metal sides and wire mesh flooring which allowed excreta to drop through onto collection trays. A black plastic tarp was placed around the crates during the feeding trials to minimize disturbance to the birds. Herons were habituated to the collection crates during the month preceding experimentation by housing them in the crates for several 24 h periods.

Feeding trials consisted of: (1) a 24 h fasting period to empty the herons' digestive tracts, (2) a single feeding of a known mass of test fish and (3) a 24 h excreta collection

period. In 1990, three species of fish (herring, mackerel and gutted trout) were tested on four herons at four intake levels (0, 50, 100 and 150 g). For each fish species, a total of eight trials were conducted, such that each bird was tested at two intake levels per fish species (intake levels were randomly assigned). Herring was tested first, followed by mackerel and gutted trout. Herons were reluctant to eat more than 150 g of fish while in the collection crates. In 1991, 11 herons were fed 0, 100, 200 or 300 g of ungutted trout. Each heron was randomly assigned to one intake level. The four birds used in 1990 were included in the 1991 trials.

Excreta, in 1990, were collected on pre-weighed aluminum-foil trays, oven dried at 60°C for 7 d, and weighed. As large a sample as possible was scraped from each tray for later nutrient analysis. In 1991, excreta were collected into a 0.5% borax solution. The excreta were freeze dried and weighed. In both years, contaminating feathers and dander were removed prior to drying. The dried excreta were stored at -20°C for later nutrient analysis.

Samples of fish were dried at 60°C for 7-14 d until mass was constant. Dried fish and excreta samples were individually ground and homogenized in a coffee grinder. Subsamples of the fish and excreta were used to determine energy content by bomb calorimetry (Leco Automatic Calorimeter model AC-300, Leco Corp., St. Joseph, Michigan) standardized with benzoic acid. A second subsample was used to measure

lipid content following Goldfisch extraction (Labconco Corp., Kansas City, Mo) with diethyl ether as a solvent. A third subsample was oxidized according to Parkinson and Allen (1975) and analyzed for nitrogen using a Technicon Autoanalyzer II (Technicon Instruments Corporation, Tarrytown, New York). A fourth subsample was ashed at 600°C in a muffle furnace for 24 h.

Total ingested energy (IE) and ingested nitrogen (IN) and total excreta energy (FE + UE) and excreta nitrogen (FN + UN) were measured for each bird on each experimental diet. Total excreta energy was regressed on IE for each experimental diet. The intercept was used to estimate endogenous excreta losses ($F_m E + U_e E$) for each test fish (Sibbald 1976, 1982). MEC was calculated using the following formulae:

$$\text{AMEC} = [\text{IE} - (\text{FE} + \text{UE})] / \text{IE} \quad (2.1)$$

$$\text{TMEC} = [\text{IE} - (\text{FE} + \text{UE}) + (\text{F}_m\text{E} + \text{U}_e\text{E})] / \text{IE} \quad (2.2)$$

AMEC and TMEC were corrected for nitrogen retention (AMEC_n and TMEC_n, respectively) as follows:

$$\text{AMEC}_n = [\text{IE} - (\text{FE}_n + \text{UE}_n)] / \text{IE} \quad (2.3)$$

$$\text{TMEC}_n = [\text{IE} - (\text{FE}_n + \text{UE}_n) + (\text{F}_m\text{E}_n + \text{U}_e\text{E}_n)] / \text{IE} \quad (2.4)$$

where:

$$(\text{FE}_n + \text{UE}_n) = (\text{FE} + \text{UE}) + 36.53 \text{ RN} \quad (2.5)$$

and:

$$\text{RN} = \text{IN} - (\text{FN} + \text{UN}) \quad (2.6)$$

The constant 36.53 kJ/g is an estimate of the energetic value for urinary nitrogen in chickens (Sibbald 1982).

Statistical analyses were performed using SYSTAT 5.1 (Wilkinson 1990). Analysis of variance was used to test for differences between the diets and the estimates of MEC, and the Least Significant Difference was used for means separation. The relationships between apparent metabolized energy [IE - (FE + UE)], apparent digested lipid (ingested lipid - lipid in excreta) and apparent retained nitrogen [IN - (FN + UN)] with the amount of the respective ingested nutrient were determined by regression analysis. Regression analysis was also used to determine the relationship between estimates of MEC and IE. Data are reported as means with 1 standard deviation.

Results

Nutrient composition of the fish varied considerably among species (Table 2.1). Herring had the highest energy density due to its high lipid content (38.6 % of dry matter), while mackerel had the lowest energy density and the lowest lipid content (16.4 % of dry matter). Energy densities of the two trout diets were intermediate between herring and mackerel.

The apparent metabolized energy, the apparent digested lipid and the apparent retained nitrogen increased linearly as the amount of the respective nutrient ingested increased, for mackerel and trout (Fig. 2.1). The apparent metabolized

Table 2.1. Nutrient composition of fish fed to the Great Blue Herons (*Ardea herodias*)^a.

Fish	n ^b	Dry			Gross	
		Mass (% WM ^c)	Nitrogen (% DM ^c)	Lipid (% DM)	Ash (% DM)	Energy (kJ/g DM)
Herring ^d	4	33.8±1.3 ^A	8.3±0.6 ^B	38.6±2.6 ^A	5.7±0.3 ^C	27.4±0.6 ^A
Mackerel ^d	4	29.1±1.1 ^B	11.8±0.8 ^A	16.4±6.0 ^C	6.8±0.7 ^B	22.7±1.0 ^C
Gutted Trout ^d	4	27.4±0.6 ^C	11.0±0.7 ^A	24.4±4.7 ^B	6.6±0.5 ^B	25.2±0.9 ^B
Ungutted Trout ^e	5	28.8±0.6 ^B	9.0±0.2 ^B	30.3±1.7 ^A	8.6±0.4 ^A	25.4±0.4 ^B

^aValues are given as means ± 1 standard deviation. Means in a given column followed by unlike letters differ significantly (P<0.05).

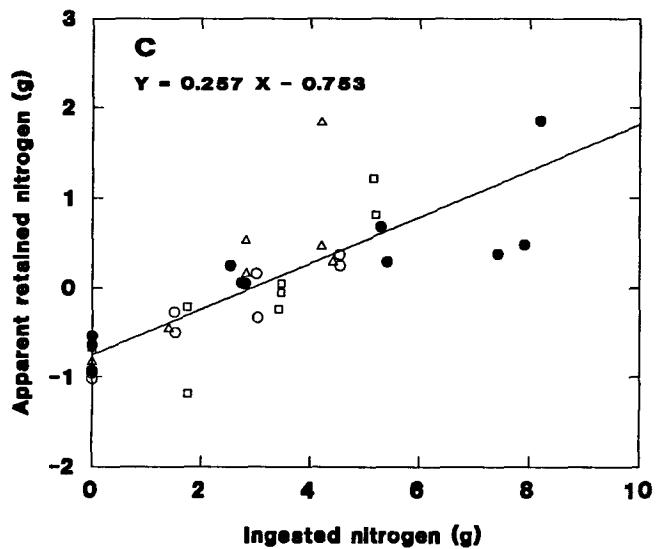
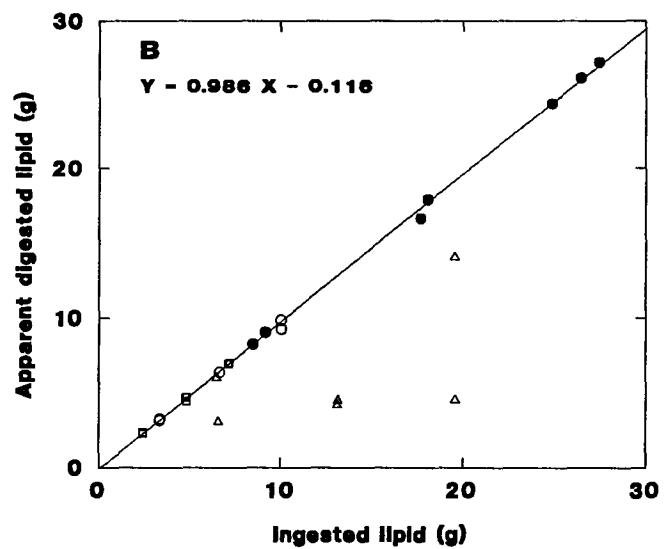
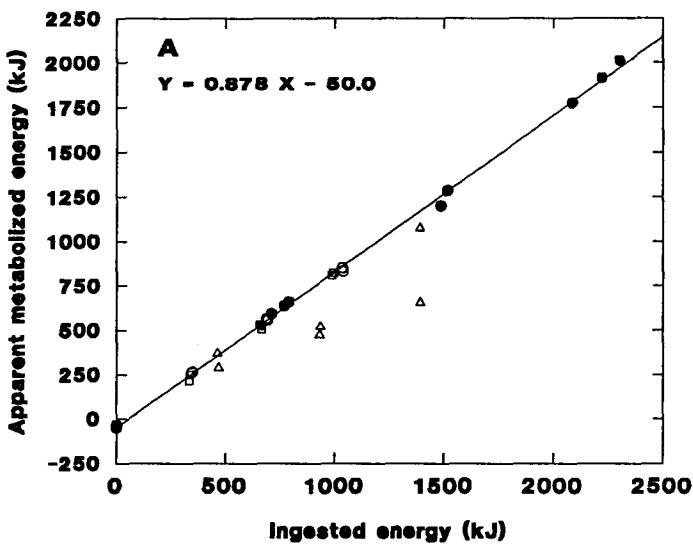
^bEach sample is a pool of two fish.

^cWM = wet mass, DM = dry mass.

^dFish fed to herons during the 1990 feeding trials.

^eFish fed to herons during the 1991 feeding trials.

Fig. 2.1. Relationships of A) apparent metabolized energy, B) apparent digested lipid, and C) apparent retained nitrogen with the amount of ingested energy, lipid, and nitrogen, respectively, for Great Blue Herons (*Ardea herodias*) fed herring (Δ), mackerel (\square) and trout (gutted \circ and ungutted \bullet). Regression equations were based on mackerel and trout for A) and B). All fish were included in the regression equation for C). Herring, mackerel and ungutted trout were fed to herons in 1990 feeding trials. Ungutted trout were fed to herons in 1991 feeding trials.



energy in relation to IE for the herring diet ($P=0.001$, $R^2 = 0.883$) was lower and more variable than the mackerel and trout diets ($P<0.001$, $R^2 = 0.999$; Fig. 2.1A). No relationship was found between the apparent digested lipid and the amount of ingested lipid for the herring diet ($P=0.287$, $R^2 = 0.273$). This relationship was significant for the mackerel and trout diets ($P<0.001$, $R^2 = 0.999$; Fig. 2.1B). The amount of nitrogen retained in relation to the amount of ingested nitrogen did not differ among the fish diets ($R^2=0.659$) (Fig. 2.1C).

The relationships between the estimates of MEC and IE for mackerel and trout (gutted and whole) are shown in Figure 2.2. AMEC and $AMEC_n$ increased significantly as IE increased ($P=0.001$, $R^2 = 0.438$ and $P=0.002$, $R^2 = 0.413$, respectively) (Fig. 2.2A and 2.2B). TMEC and $TMEC_n$ were independent of IE ($P>0.05$ for both) (Fig. 2.2C and 2.2D). For the herring diet, no consistent pattern was found between the estimates of MEC and IE (Fig. 2.3).

No significant differences were found between estimates of MEC (AMEC and TMEC) and their nitrogen-corrected equivalents for mackerel and trout (Table 2.2), but TMEC was significantly greater than AMEC for these diets. No significant differences were found among the four estimates of MEC for herring (Table 2.2).

Fig. 2.2. Effect of the amount of ingested energy on estimates of A) apparent (AMEC) and C) true (TMEC) metabolizable energy coefficients and their nitrogen-corrected equivalents (AMEC_n, TMEC_n) (B,D) of three fish diets (mackerel □, gutted trout ○ and ungutted trout ●) when fed to Great Blue Herons (*Ardea herodias*). Mackerel and ungutted trout were fed to herons in 1990 feeding trials. Ungutted trout were fed to herons in 1991 feeding trials.

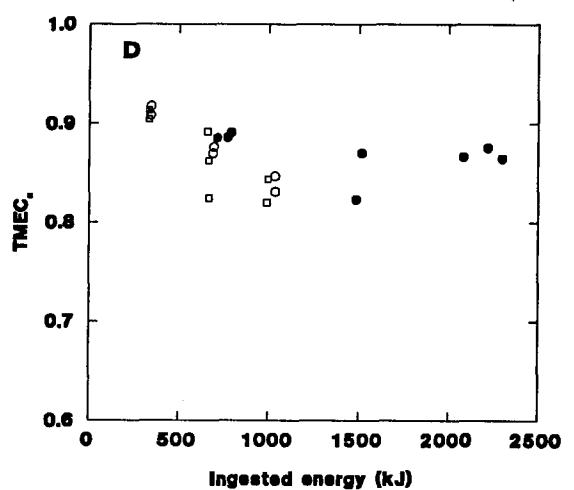
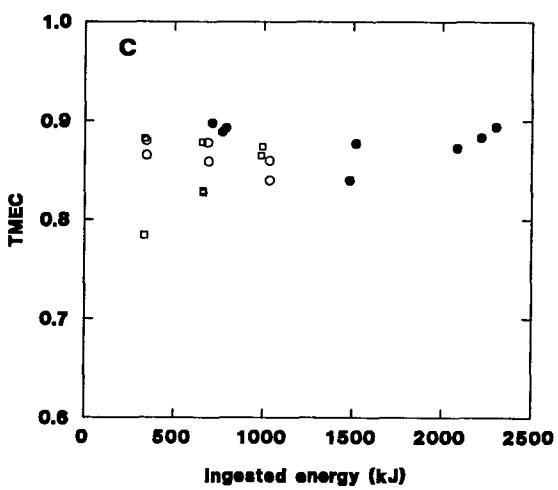
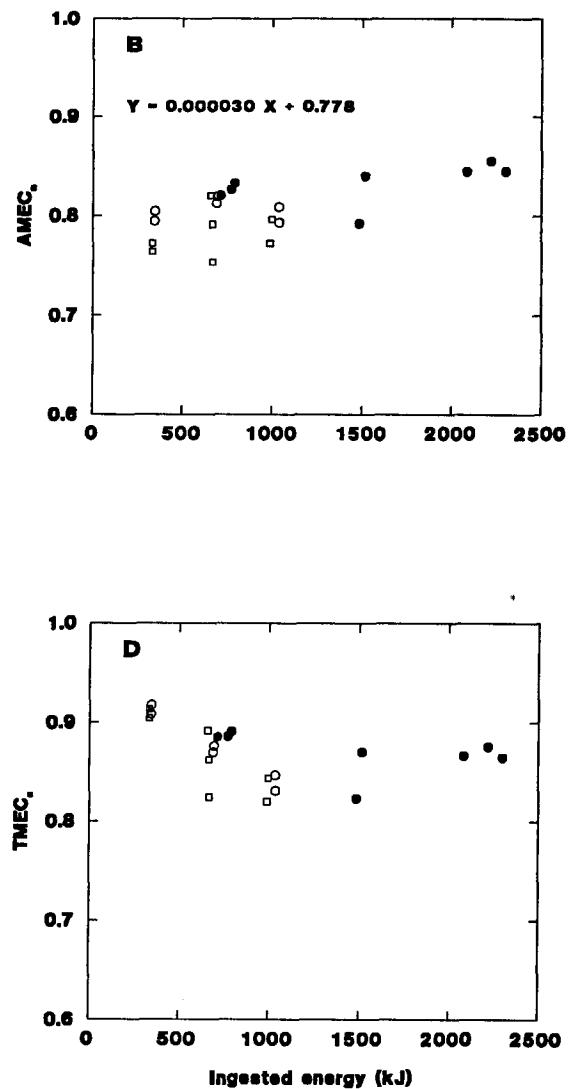
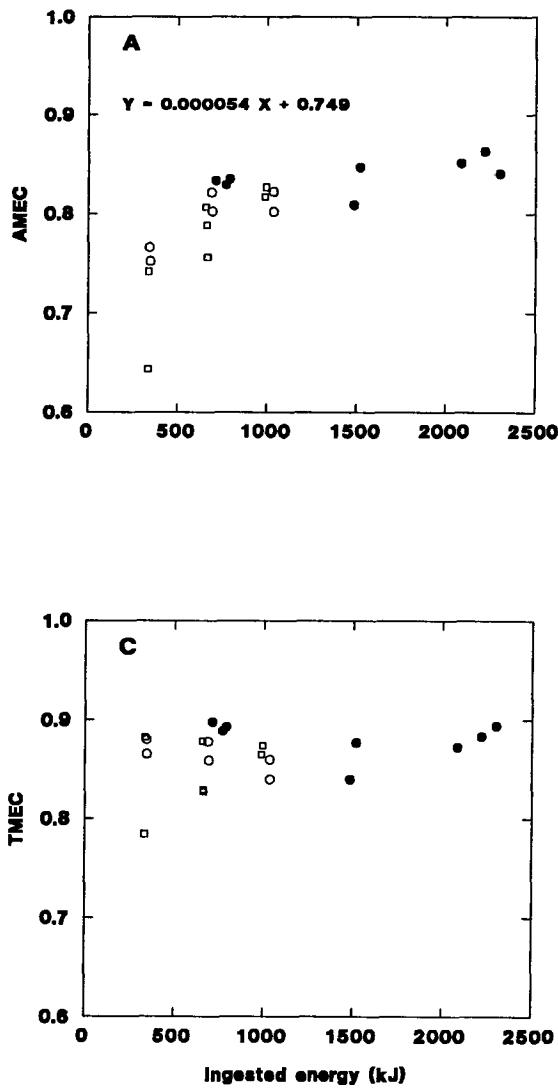


Fig. 2.3. Effect of the amount of ingested energy on estimates of apparent (AMEC ○) and true (TMEC □) metabolizable energy coefficients and their nitrogen-corrected equivalents (AMEC_n ●, TMEC_n ■) of herring (1990 feeding trials) when fed to Great Blue Herons (*Ardea herodias*).

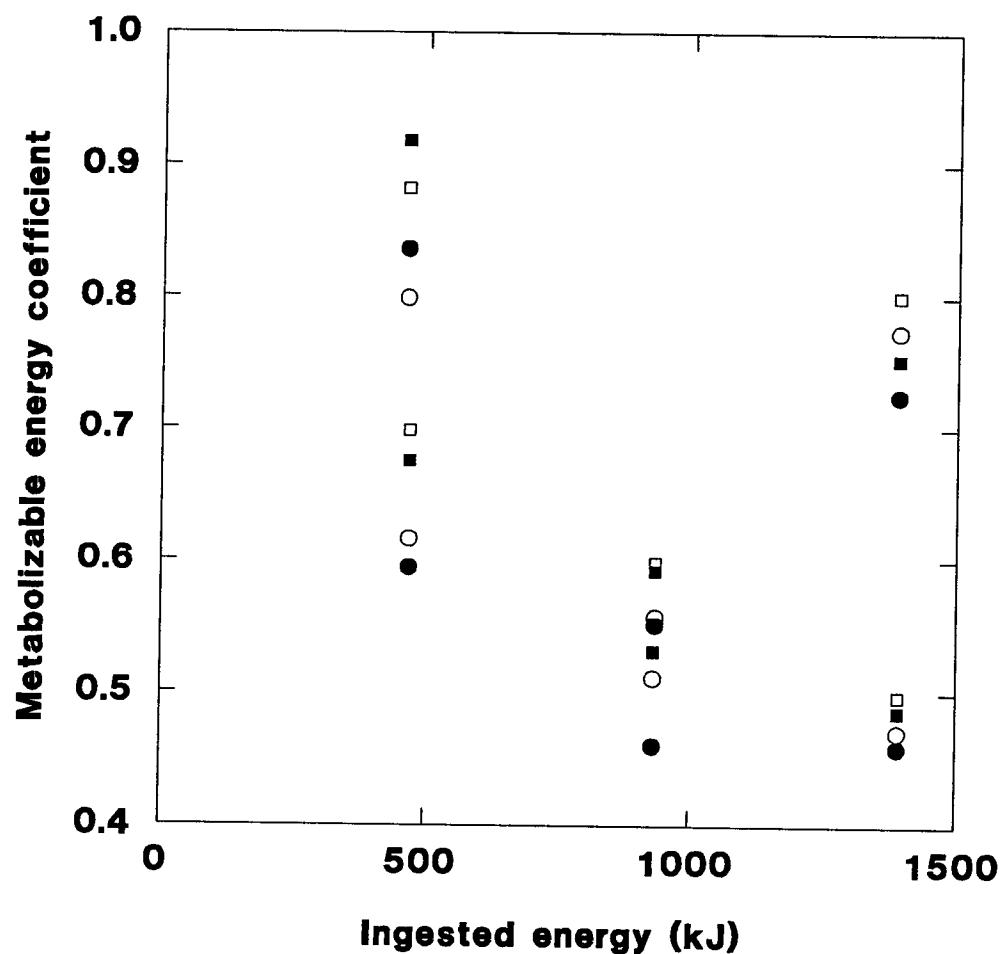


Table 2.2. Metabolizable energy coefficients (MEC) of fish when fed to Great Blue Herons (*Ardea herodias*)^a.

	Herring ^b	Mackerel ^b	Gutted Trout ^b	Whole Trout ^c
Apparent MEC	0.621±0.137 ^A	0.769±0.063 ^B	0.794±0.029 ^B	0.842±0.020 ^B
Apparent MEC _n ^d	0.609±0.145 ^A	0.781±0.022 ^B	0.806±0.010 ^B	0.832±0.019 ^B
True MEC	0.671±0.149 ^A	0.853±0.035 ^A	0.864±0.015 ^A	0.881±0.019 ^A
True MEC _n ^d	0.659±0.159 ^A	0.866±0.038 ^A	0.875±0.034 ^A	0.870±0.021 ^A

^aValues are given as means ± 1 standard deviation. Means in a given column followed by unlike letters differ significantly (P<0.05).

^bFish fed to herons in 1990 feeding trials. For each fish species, eight trials were conducted (four birds and four intake levels of fish, such that each bird was tested at two intake levels per fish species).

^cFish fed to herons in 1991 feeding trials. A total of 11 trials were conducted (11 herons and four intake levels, such that each heron was tested at one intake level).

^dNitrogen corrected metabolizable energy coefficient.

Discussion

Apparent metabolizable energy coefficients of mackerel and trout determined in the present study were within the range of AMEC of fish for many species of birds (Table 2.3). The average AMEC of fish when fed to birds is 0.775 ± 0.053 (Heath and Randall 1985; Jackson 1986; Castro et al. 1989; Robertson and Newgrain 1992; present study). AMEC, however, underestimated the MEC of the test fish by 3.8-8.4%, as predicted by TMEC (Table 2.2). Since AME estimates fail to recognize $F_m E + U_e E$ as endogenous losses, FE + UE of dietary origin is overestimated (Sibbald 1982) and consequently MEC is underestimated. Thus, when MEC values are used to convert energy budgets into food requirements, this underestimation results in an overestimation of the amount of food required to meet a bird's energy needs.

Variation in IE has been shown to affect estimates of AME but not TME (Sibbald 1975, 1976; Wolynetz and Sibbald 1984) because $F_m E + U_e E$ make up an increasing proportion of FE + UE as IE declines. In theory, AMEC approaches TMEC as IE increases, but even when measured at maintenance (IE that maintains body mass) TMEC exceeds AMEC by 3% (Miller and Reinecke 1984). In the present study, the differences between AMEC and TMEC were greater than 3% because most of the feeding trials were conducted below the maintenance energy requirements of the captive herons (estimated to be

Table 2.3. Apparent metabolizable energy coefficients (AMEC) of fish fed to birds*.

Species of bird	Species of fish	AMEC	Reference
Sphenisciformes			
<i>Aptenodytes forsteri</i>	pilchards	0.818	Robertson and Newgrain 1992
<i>Pygoscelis adeliae</i>	unknown	0.800	Kooyman <i>et al.</i> 1982
<i>Spheniscus demersus</i>	anchovy	0.753	Cooper 1977
<i>S. demersus</i>	anchovy	0.78-0.88	Heath and Randall 1985
<i>S. demersus</i>	mullet	0.77-0.87	Heath and Randall 1985
Procellariiformes			
<i>Procellaria aequinoctialis</i>	light-fish	0.779	Jackson 1986
Pelecaniformes			
<i>Morus capensis</i>	anchovy	0.761	Cooper 1978
<i>M. capensis</i>	anchovy	0.746	Cooper 1978
<i>M. capensis</i>	pilchard	0.794	Batchelor and Ross 1984
<i>M. capensis</i>	stockfish	0.692	Batchelor and Ross 1984
<i>Pelecanus onocrotalus</i>	fish	0.730	Cooper 1980
<i>Phalacrocorax auritus</i>	pollack	0.849	Dunn 1975a
Ciconiformes			
<i>Ardea herodias</i>	herring	0.621	This study
<i>A. herodias</i>	mackerel	0.769	This study
<i>A. herodias</i>	gutted trout	0.794	This study
<i>A. herodias</i>	whole trout	0.842	This study
<i>Eudocimus albus</i>	shelled shrimp and anchovy	0.68-0.92	Kushlan 1977a
<i>Mycteria americana</i>	whiting	0.790	Kahl 1964
Falconiformes			
<i>Haliaeetus leucocephalus</i>	salmon	0.750	Stalmaster and Gessaman 1982
Charadriformes			
<i>Rissa tridactyla</i>	fish	0.76	Gabrielsen <i>et al.</i> 1987

*After Castro *et al.* 1989.

approximately 1430 kJ/d, Chapter 4). My data provides support for the recommendation by Miller and Reinecke (1984) that AMEC estimates should be obtained only from birds fed at maintenance levels. However, feeding trials designed to measure AMEC are often impractical for use on wild birds (Miller and Reinecke 1984). Measurement of TMEC, based on the TME assay of Sibbald (1976) provides a simple rapid alternative which yields estimates of MEC that are independent of IE, and more accurately reflect the efficiency with which a bird is able to convert gross energy of the diet into usable energy.

Correcting for nitrogen retention did not improve the estimates of MEC in this study (Table 2.2) and there was a tendency for $TMEC_n$ to be overestimated at low IE (Fig 2.2D). Previous studies have shown that when RN is negative (ie. when IE is below maintenance) $AME_h > AME$ and $TME_h < TME$, and when RN is positive the opposite is true. This is because estimates of $FE_n + UE_n$ vary in relation to the amount of tissue protein catabolized (Wolynetz and Sibbald 1984; Sibbald and Wolynetz 1985). However, this was not the case in the present study, since the amount of nitrogen in the excreta was probably overestimated, due to feather and dander contamination. As a result $FE_n + UE_n$ was probably underestimated resulting in an overestimate of MEC_n . This would have been particularly true at low IE, where feather and dander contamination made up a larger relative portion of the collected excreta.

MEC of herring was difficult to estimate (Table 2.2, Fig. 2.3) because of variability in apparent lipid digestibility (Fig. 2.1B). The herring may have become rancid, resulting in decreased digestibility of the lipid fraction (March et al. 1962; Carpenter et al. 1966; Squires et al. 1991) and reduced palatability (Carpenter et al. 1966). As herring was the first fish tested in the 1990 feeding trials, the reluctance of herons to eat more than 150 g of fish may have been due to the herons associating the feeding trials with the herring. Herons were willing to eat more than 150 g of trout in the 1991 feeding trials. The quality (ie. degree of oxidative rancidity) of the fish in the present study was not measured. The herring used in this study had been stored frozen for approximately 8 months, while the mackerel and trout were stored frozen for less than 2 months. Our estimate of AMEC of herring fed to herons is the lowest reported MEC of fish for birds (Table 2.3).

The method of excreta treatment was changed from collection on aluminum-foil trays followed by oven drying (1990) to collection into a 0.5% borax solution followed by freeze drying (1991). The results from both years showed similar patterns of apparent retained nitrogen in relation to the amount of nitrogen ingested (Fig. 2.1C), negating our concern about nitrogen loss. Shannon and Brown (1969) found similar losses of nitrogen (less than 5%) when poultry excreta were either freeze dried or oven dried at 60°C.

In this study the MEC of fish when fed to captive Great Blue Herons was measured. TMEC, in comparison with AMEC, more accurately reflected the efficiency with which gross energy of the diet was converted into usable energy by captive herons.

CHAPTER 3

**GROWTH AND ENERGY REQUIREMENTS OF HAND-
REARED GREAT BLUE HERON (*ARDEA HERODIAS*) CHICKS**

Introduction

Reproductive success of Great Blue Herons (*Ardea herodias*) is thought to be limited by the parents' ability to gather food (Powell 1983; Sullivan 1988). Starvation appears to be the primary cause of nestling mortality (Collazo 1981; Quinney 1982; Pratt and Winkler 1985). Great Blue Heron eggs hatch asynchronously, resulting in the establishment of a size hierarchy among siblings (Quinney 1982; Mock 1985, 1987). The largest chicks get most of the food (Mock 1985, 1987). As a result, younger chicks grow more slowly and usually die of starvation (Quinney 1982).

An understanding of the energy requirements of chicks in relation to the parents' ability to provide food is needed to fully evaluate energy limitations on reproductive success. Little is known about energy requirements of Great Blue Heron chicks. The peak number of feeding visits by parents occurs at about 29 days after hatch (Dowd and Flake 1985). Parents ingest more energy when feeding small chicks than large chicks (Butler 1991b).

Quinney (1982) found body mass of wild Great Blue Heron chicks during the first month of life increased in a nearly linear manner and that no discernible sexual dimorphism occurred during this time. However, adult male herons are about 17 % heavier than adult female herons (Hartman 1961; Simpson 1984). The age at which Great Blue Herons become sexually dimorphic has not been reported.

The objectives of this study were: 1) to describe growth in hand-reared Great Blue Heron chicks, 2) to estimate the energy requirements of Great Blue Heron chicks, and 3) to construct an energy budget for Great Blue Heron chicks.

Materials and methods

Animals and rearing procedures

Eggs were collected from three Great Blue Heron colonies in south-western British Columbia in April 1991. Eggs were incubated and hatched in a Petersime #1 Tabletop Incubator at 37.5°C dry bulb and 30°C wet bulb (Hart et al. 1991). Chicks remained in the incubator for up to 24 h after hatching.

Chicks were brooded in pairs in open clear plastic boxes (26.7 x 16.5 x 12.1 cm) lined with twigs and paper towels. Chicks were initially brooded at 36°C. The temperature was reduced by approximately 1°C per day until room temperature (20°C) was reached. The brooder temperature regime was established by observing the chicks for signs of heat or cold stress (e.g. gular fluttering, huddling) and adjusting the temperature accordingly. Chicks were transferred to wood-framed nest boxes when they were 2-3 wk old. Lighting was provided by wide spectrum fluorescent light bulbs with the photoperiod controlled to coincide with the natural photoperiod. Chicks were transferred to an outdoor aviary (100 x 50 x 3 m) when the youngest chick was older than 50 d of age, corresponding to the age when heron chicks climb out

of nests onto tree limbs (Butler 1989).

Chicks were hand-fed salmonids (*Oncorhynchus* sp.; Table 3.1) as a ground homogenate or as whole fish to satiation four times per day. Coho salmon (*O. kisutch*), spring salmon (*O. tshawytscha*) and rainbow trout (*O. mykiss*) were fed to chicks 0-5, 6-10, and 11-75 d of age, respectively (day 0 was the hatching date). Drinking water was not provided until chicks were in the outdoor pens.

Nutrient analyses

Samples of fish were analyzed for energy, lipid and ash content as described in Chapter 2. Protein content of the fish was determined as the lean ash-free dry mass (100 % - % Lipid - % Ash).

Growth

Chicks were weighed individually to the nearest 0.1 gram (Sartorius scale, model I 6800 A) each day prior to the first feeding. The relationship between chick mass (M, g) and age (t, days) was described using the logistic equation:

$$\begin{aligned} M &= A / (1 + (be^{-kt})) \\ b &= (A-i)/i \end{aligned} \quad (3.1)$$

where A = the asymptotic mass, i = the hatching mass and k = the logistic growth rate (day⁻¹; Ricklefs 1983). The daily mass gain (G, g/d) was calculated as the difference between the mass on consecutive days. The absolute growth rate (AGR, g/d) was calculated as the average daily mass gain during the linear period of growth (Drent and Daan 1980).

Table 3.1. Nutrient composition of fish fed to the Great Blue Heron (*Ardea herodias*) chicks^a.

Fish	n ^b	Dry			Gross	
		Mass (% WM ^c)	Lipid (% DM ^c)	Ash (% DM)	Protein ^d (% DM)	Energy (kJ/g DM)
Coho salmon	3	21.8±1.4	19.5±2.1	12.0±1.2	68.4±1.7	22.6±0.8
Spring salmon	6	30.6±1.5	35.3±1.5	5.9±0.4	58.9±1.3	27.2±0.3
Rainbow trout	12	29.5±0.7	29.9±1.2	8.7±0.2	61.4±1.0	25.0±0.2

^aValues are given as means ± SEM.

^bEach sample is a pool of two fish.

^cWM = wet mass, DM = dry mass.

^d% Protein = 100 % - (% Lipid) - (% Ash).

Energy requirements

Food consumption was measured by weighing the chicks or the food bucket plus fish before and after each feeding, the difference being the wet mass of food consumed. Gross energy intake was calculated by multiplying the wet mass of fish consumed by the % dry matter and gross energy content of the fish (Table 3.1). Adult herons, on average, metabolize 86.6 % of the energy in fish diets (Chapter 2). Assuming chicks have a similar efficiency (Sibbald 1978; Shires et al. 1980), the metabolizable energy intake (E_{ME} ; kJ/d) of the heron chicks was calculated by multiplying the gross energy intake by a true metabolizable energy coefficient (MEC) of 0.866.

The energy requirements for maintenance (E_{MAIN}) and gain (E_{GAIN}) were determined using the method of Hurwitz et al. (1978). Their model states that the total metabolizable energy requirement (E_{TOT} , kJ/d) of a growing animal is the sum of E_{MAIN} and E_{GAIN} and assumes that: 1) E_{MAIN} and E_{GAIN} are independent constants, 2) E_{MAIN} is a function of metabolic body mass ($M^{0.67}$), and 3) the type of gain is homogeneous relative to age (ie. within a measurement period) (Hurwitz et al. 1978). The model is expressed as:

$$E_{TOT} = E_{MAIN}M^{0.67} + E_{GAIN}G \quad (3.2)$$

which can be linearized to:

$$E_{TOT}/G = E_{MAIN}M^{0.67}/G + E_{GAIN} \quad (3.3)$$

where E_{MAIN} is estimated by the slope and is expressed as kJ per gram metabolic body mass per day ($\text{kJ/g}^{0.67}/\text{d}$), and E_{GAIN} is

estimated by the intercept of this relationship and is expressed as kJ per gram body mass gain per day (kJ/g/d). EI_{ME} was substituted into equation 3.3 for E_{TOT} (Hurwitz et al. 1978).

The method of Hurwitz et al. (1978) was modified by calculating the energy requirements of individual chicks at 10 day intervals between the ages of 10 and 70 days. This was done in order to: 1) minimize violating assumption 3 (homogenous gain) of the method of Hurwitz et al. (1978), and 2) determine whether there were sex and developmental differences in energy requirements of heron chicks. Data from the first 10 days were excluded from the analysis to remove any biases due to potential utilization of yolk, which reduces the chicks' dependence on dietary energy sources (Hurwitz et al. 1978). Chicks were unable to maintain body temperature throughout the day at this time (Calogeros et al., unpublished data) and relied on external heat sources for warmth.

Energy budgets were constructed for male and female heron chicks between the ages of 10 and 70 d. For each 10 d period, the mean body mass and body mass gain were calculated for male and female chicks. The total energy needs for maintenance and gain were then calculated on a whole bird basis for each period (ie. $M^{0.67} \times E_{MAIN}$ and $G \times E_{GAIN}$, respectively). Since herons, on average, metabolize 86.6 % of the gross energy in fish diets (Chapter 2), excreta losses were assumed to account for 13.4 % of the gross energy intake of the chicks. For

details of the calculation procedures see Table 3.3.

Sex determination

Blood samples from heron chicks were sent to Zoogen Inc. (Davis, California) for sex determination by restricted fragment length polymorphism analysis.

statistical analyses

Statistical analyses were performed using SYSTAT 5.1 (Wilkinson 1990). The logistic equation (Eq. 3.1) was fit by nonlinear estimation, while Hurwitz's equation (Eq. 3.3) was fit by linear regression. Sex differences in body mass, EI_{ME} and growth rates were analyzed by t-tests. Sex and developmental differences in energy requirements were analyzed by the following statistical model:

$$Y_{ij} = \mu + S_i + P_j + (SP)_{ij} + e_{ij} \quad (3.4)$$
$$i = 1, 2; \quad j = 1, 2, 3, 4, 5, 6$$

where Y_{ij} = the energy requirement for maintenance or gain, S_i = the sex of the chick, P_j = the developmental period, $(SP)_{ij}$ = the interaction between sex and period, and e_{ij} = error term. The Least Significant Difference test was used for means separation. If no sex differences were found data from all 12 birds were pooled. Data are reported as means \pm SEM.

Results

Growth

The hatching mass of male herons (54.2 ± 1.6 g; n=8) was 2.9 % greater than female herons (52.6 ± 0.9 g; n=4), but the difference was not significant ($P=0.41$). However, the asymptotic masses, as determined by logistic curves, were about 12 % greater for male chicks (2465 ± 51 g) than for female chicks (2179 ± 10 g) and this difference was significant ($P=0.001$) (Fig 3.1). As expected, the growth rate of male herons ($k = 0.167 \pm 0.004 \text{ d}^{-1}$ and AGR = $70.7 \pm 4.1 \text{ g/d}$) was significantly different (k : $P=0.03$; AGR: $P<0.001$) from the growth rate of female herons ($k = 0.178 \pm 0.003 \text{ d}^{-1}$ and AGR = $60.5 \pm 0.4 \text{ g/d}$). Both sexes reached their asymptotic mass by 60 d of age (Fig. 3.1).

Energy requirements

Daily EI_{ME} increased with age up to 26 d, remained relatively constant at 2027 ± 25 kJ for the next 16 d (26 to 41 days) and decreased to 1545 ± 22 kJ by day 50 (Fig. 3.2). Daily EI_{ME} was not significantly different ($P>0.05$) between males and females.

There was no significant interaction between sex and developmental period for either E_{MAIN} or E_{GAIN} ($P=0.24$ and $P=0.74$, respectively). Both E_{MAIN} and E_{GAIN} varied significantly among developmental periods ($P=0.004$ and $P=0.032$, respectively), but not between males and females ($P=0.56$ and $P=0.61$, respectively). Energy requirements are listed in

Figure 3.1. Body mass of A) male (n=8) and B) female (n=4) hand-reared Great Blue Heron (*Ardea herodias*) chicks as a function of age. Values are given as means \pm SEM. The solid lines represent the growth curves described by the logistic equations.

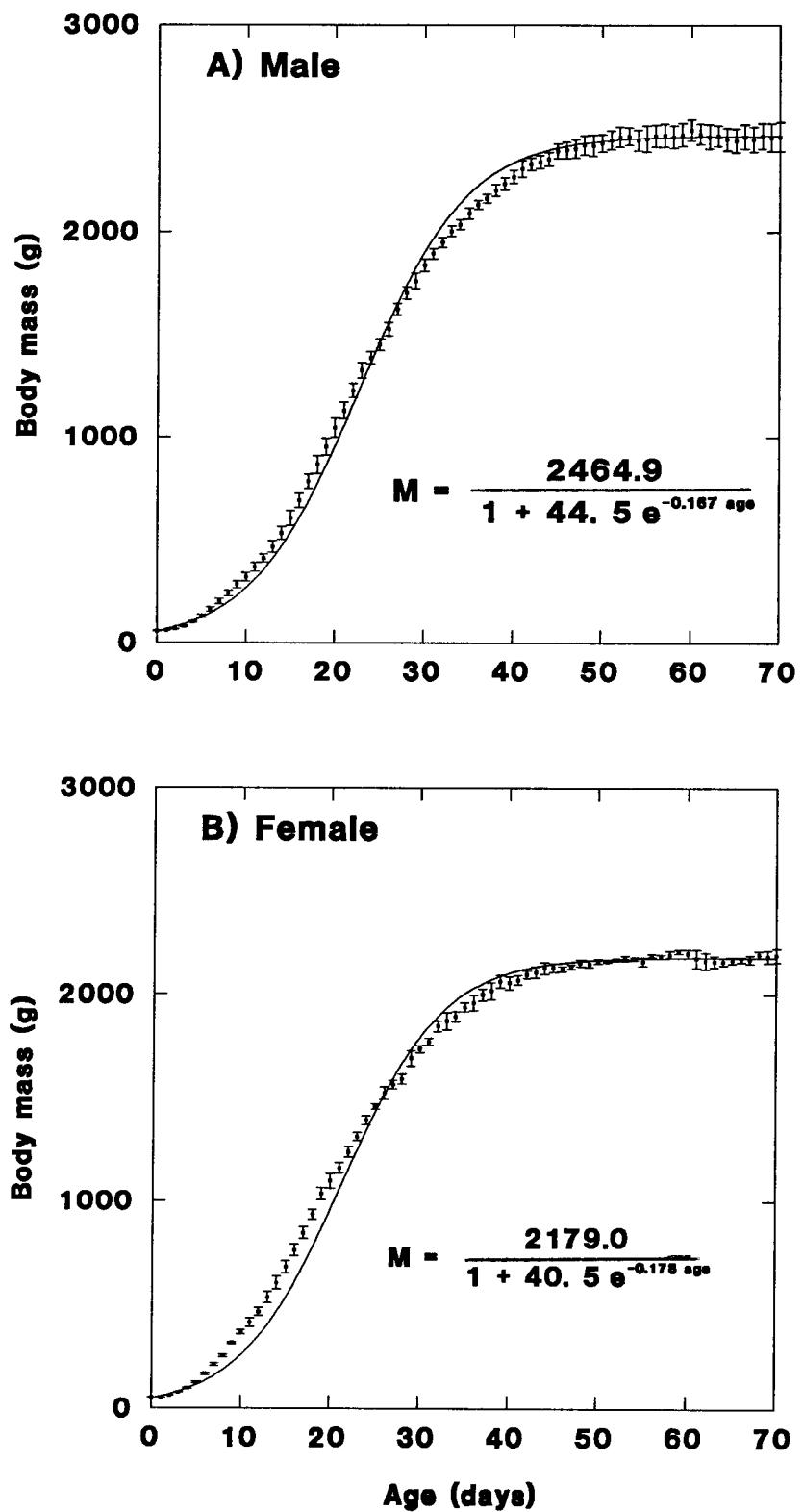


Figure 3.2. Daily metabolizable energy intake of hand-reared Great Blue Heron (*Ardea herodias*) chicks (n=12) as a function of age. Values are given as means \pm SEM.

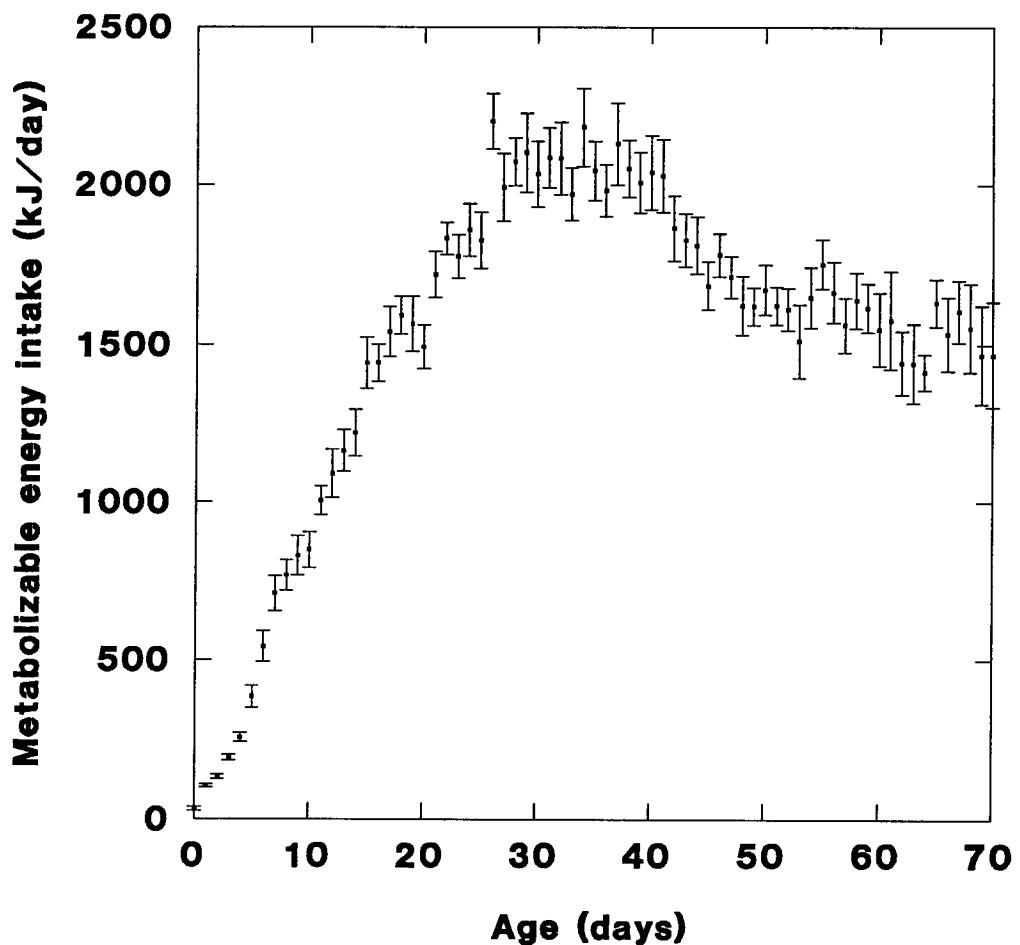


Table 3.2.

Energy budgets of male and female heron chicks followed similar patterns (Table 3.3, Fig. 3.3) and the total gross energy requirement predicted by these budgets reflected the observed gross energy intake of the chicks (Fig. 3.3). As the chicks grew, their total gross energy requirement and total energy requirement for maintenance increased to a maximum between 30 and 39 d of age and declined thereafter. The total energy requirement for gain was greatest between 10 and 19 d of age for female chicks and 10 and 29 d of age for male chicks. During the times of maximum growth (days 10-20) and maximum energy needs (days 30-40), energy requirements for gain accounted for 35.8 and 14.2 % of the chicks' total gross energy needs, respectively.

Table 3.2. Energy requirements for maintenance and gain of hand-reared Great Blue Heron (*Ardea herodias*) chicks (n=12) as a function of age^a.

Age			
Interval		E_{MAIN}^b	E_{GAIN}^c
	(days)	(kJ/g ^{0.67} /day)	(kJ/g/day)
10-19		10.79 ± 0.86 ^{AB}	7.82 ± 0.98 ^A
20-29		10.98 ± 0.83 ^A	7.57 ± 0.63 ^A
30-39		10.39 ± 0.29 ^{AB}	8.90 ± 0.46 ^A
40-49		9.30 ± 0.23 ^{BC}	11.19 ± 1.59 ^B
50-59		8.47 ± 0.26 ^C	8.32 ± 1.12 ^A
60-70		8.21 ± 0.23 ^C	9.70 ± 1.42 ^A

^aEnergy requirements were determined using the method of Hurwitz et al. (1978) (See text for details). Values are given as means ± SEM. Means in a given column followed by unlike letters differ significantly (P<0.05).

^b E_{MAIN} = energy requirement for maintenance, expressed as kJ per gram metabolic body mass (g^{0.67}) per day.

^c E_{GAIN} = energy requirement for gain, expressed as kJ per gram body mass gain per day.

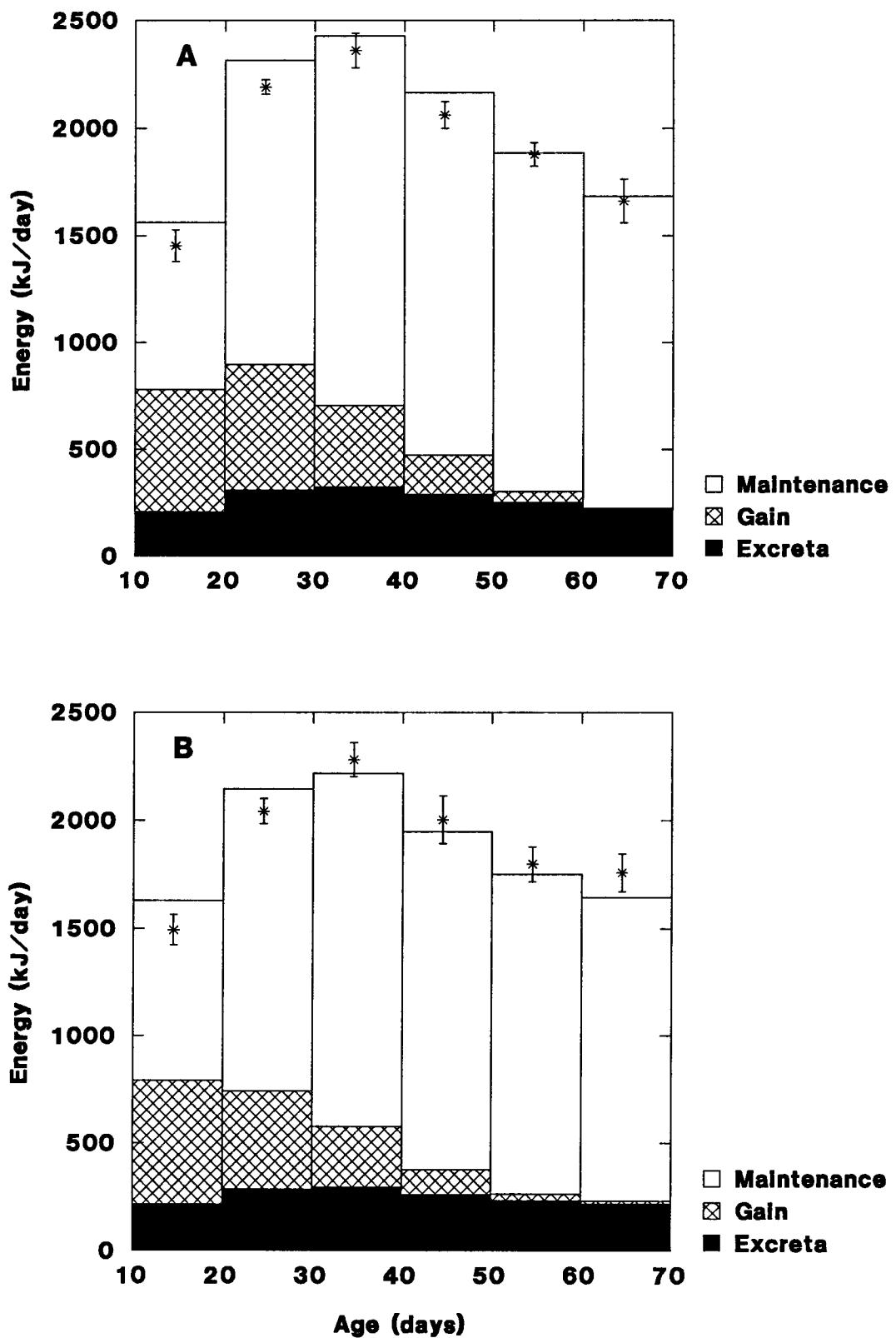
Table 3.3. Calculation of the energy budgets (modelled after Ricklefs et al. 1980) of male and female hand-reared Great Blue Heron (*Ardea herodias*) chicks^a.

Age Interval (days)	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
Male chicks									
10-19	597	73.0	10.79	7.82	781	571	1352	209	1561
20-29	1416	77.4	10.98	7.57	1418	587	2005	310	2315
30-39	2053	42.7	10.39	8.90	1722	380	2102	325	2427
40-49	2361	16.4	9.30	11.19	1693	183	1876	290	2166
50-59	2455	6.2	8.47	8.32	1581	52	1633	253	1886
60-70	2462	-8.2	8.21	9.70	1537	-80	1457	226	1682
Female chicks									
10-19	665	73.3	10.79	7.82	840	573	1413	219	1632
20-29	1396	60.1	10.98	7.57	1405	455	1860	288	2148
30-39	1912	31.6	10.39	8.90	1642	281	1923	298	2221
40-49	2115	10.4	9.30	11.19	1572	116	1688	261	1950
50-59	2177	3.7	8.47	8.32	1488	31	1518	235	1753
60-70	2174	1.1	8.21	9.70	1414	11	1425	220	1646

^aExplanation of columns:

- (1) Actual mean body mass (g)
- (2) Actual mean body mass gain (g/day)
- (3) Energy requirement for maintenance (kJ/g^{0.67}/day) from Table 3.2
- (4) Energy requirement for gain (kJ/g/day) from Table 3.2
- (5) Total energy requirement for maintenance (kJ/day) = (1)^{0.67} x (3)
- (6) Total energy requirement for gain (kJ/day) = (2) x (4)
- (7) Total metabolizable energy requirement (kJ/day) = (5) + (6)
- (8) Total excreta energy (kJ/day) = 0.134 x (7)/0.866
- (9) Total gross energy requirement (kJ/day) = (7)/0.866

Figure 3.3. Energy budgets for A) male (n=8) and B) female (n=4) hand-reared Great Blue Heron (*Ardea herodias*) chicks. Budget calculations are presented in Table 3.3. The star symbols represent the observed gross energy intakes (means \pm SEM) of chicks.



Discussion

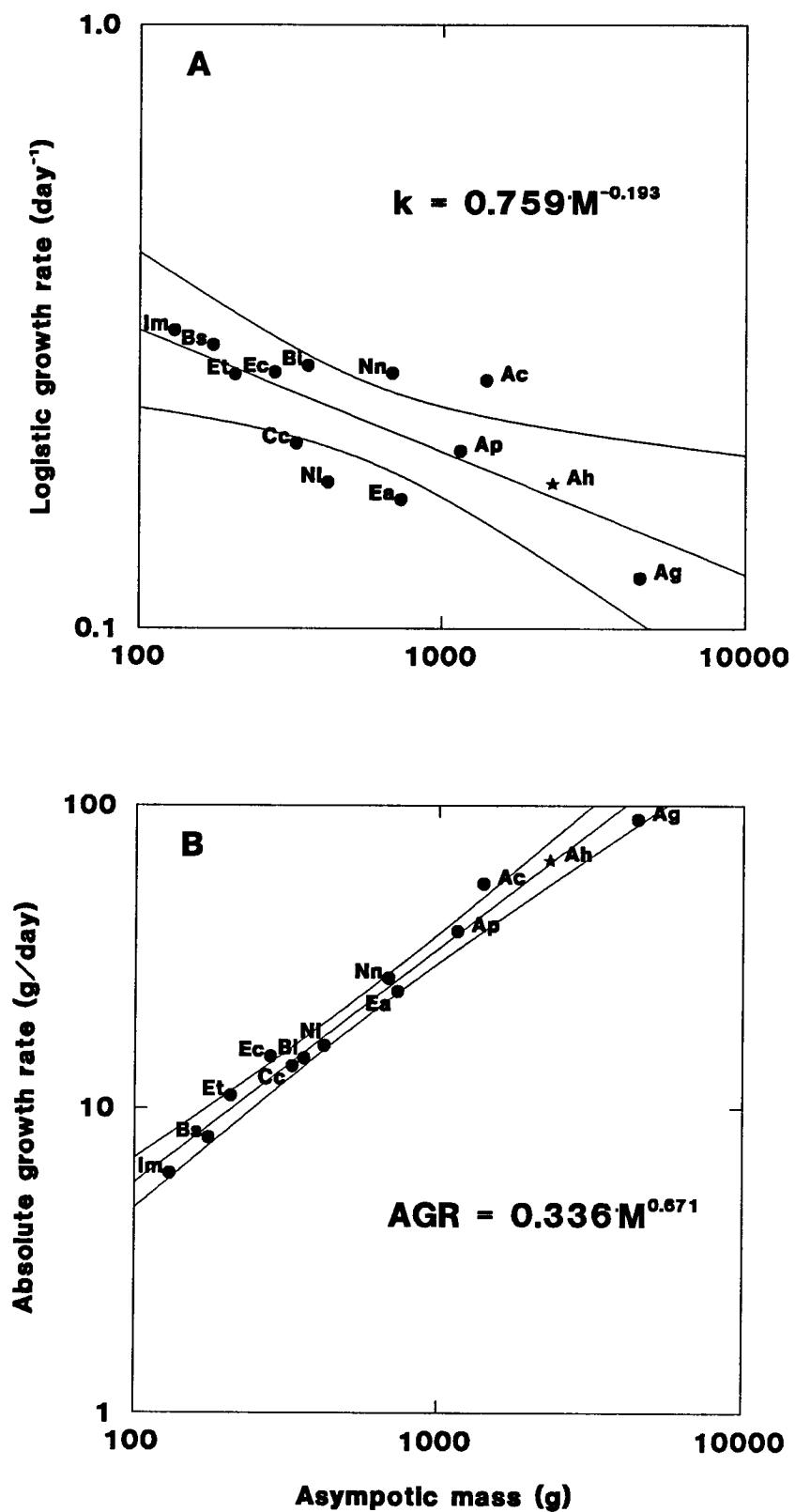
Growth of hand-reared Great Blue Heron chicks in the present study was similar to that of studies of wild nestlings (McAloney 1973; Quinney 1982). The relationship between growth rate and asymptotic mass of 13 heron species (body mass range 130–4500 g) indicates that the hand-reared Great Blue Herons in the present study grew at a rate to be expected for herons fledging at a mass of 2.3 kg (Fig. 3.4). These comparisons support the contention that my method of hand-rearing heron chicks provides a suitable model to study the growth and energy requirements of wild Great Blue Heron nestlings.

Energy requirements

Maintenance energy requirements determined in this study (Table 3.2) include the requirements for basal metabolism, thermoregulation and voluntary activity (Harris 1966; Ricklefs 1974; Kendeigh et al. 1977). Thermoregulation can be a major component in the maintenance energy requirement of nestlings, however, heron chicks in the present study were raised under relatively constant temperatures and presumably within their thermoneutral zone. Therefore, maintenance energy requirements determined in this study would contain a minimal thermoregulatory component.

E_{MAIN} ($\text{kJ/g}^{0.67}/\text{day}$) declined as the birds grew (Table 3.2). This decline may represent an accumulation of metabolically inactive tissues, such as adipose, feathers and

Figure 3.4. The relationship between A) logistic growth rate (k) and B) absolute growth rate (AGR) with asymptotic body mass (M) for various species of herons (see Appendix 2 for data and sources). The star symbol represents the growth rates of hand-reared Great Blue Heron (*Ardea herodias*) chicks determined in the present study. Key to species: *Ardea cinerea* (Ah), *A. goliath* (Ag), *A. purpurea* (Ap), *A. herodias* (Ah), *Bubulcus ibis* (Bi), *Butorides striatus* (Bs), *Cochlearius cochlearius* (Cc), *Egretta alba* (Ea), *E. caerulea* (Ec), *E. thula* (Et), *Ixobrychus minutus* (Im), *Nycticorax nycticorax* (Nn) and *N. leuconotus* (Nl).



skeleton. The energy requirement for gain (kJ/g gain/day) was greatest between 40 and 49 d, but did not differ significantly among the rest of the development periods (Table 3.2).

Total gross energy requirements of the chicks were relatively low during their first 20 d (Table 3.3, Fig. 3.3). Low energy requirements of chicks should enable parents to spend less time foraging and more time brooding their young. Heron chicks are brooded by their parents for 2 wk after hatching (McAloney 1973) and are not fully homeothermic until 3 wk of age (Calogeros et al., unpublished data). During the chicks' first 3 weeks female herons mostly feed the chicks (Butler 1991b) and at least one parent remains in constant attendance (Pratt 1970). Parents seldom leave the chicks unattended to forage for chicks until the young are 3 wk old, which coincides with the time of maximum energy requirements of the chicks (Fig. 3.3).

Energy limitation and reproductive success

Food consumption was greatest between 4 and 6 wk of age, during which time chicks consumed 2027 ± 25 kJ/d (Fig. 3.2). Sullivan (1988) showed that broods of four chicks were fed more often than broods where three chicks were fledged, with no difference in the provisioning rate per chick. Therefore, parents must provide about 6100 and 8100 kJ/d during the period of maximum energy intake to support a brood of three and four nestlings, respectively, in addition to providing for

their own energy requirements.

The estimated maintenance requirements of adults was calculated by multiplying the total gross energy requirements for maintenance of captive herons between 8 and 20°C (1434 kJ/d, calculated in Chapter 4) by the MEC of fish when fed to herons (0.866, calculated in Chapter 2). Assuming the total metabolizable energy requirements of wild ciconiiformes to be 1.5 times maintenance requirements (Kahl 1964; Siegfried 1969; Kushlan 1977b), the metabolizable energy requirement of adult Great Blue Herons is 1863 kJ/d. Assuming both parents contribute equally to feeding the chicks (Butler 1991b), the above provisioning levels (6100 kJ/brood of three chicks and 8100 kJ/brood of four chicks) represent a 2.6 and 3.2 fold increase, respectively, in the amount of ME that the parents must obtain in order to meet the energy needs of themselves and their chicks during the time of peak energy consumption of the chicks.

Butler (1991b) estimated that the metabolizable energy intakes of adult herons were 4796 ± 859 and 1797 ± 170 kJ/d (mean \pm SD) when small and large chicks, respectively, were in the nests [these estimates were adjusted from an apparent MEC of 0.77 (Castro et al. 1989) to a true MEC of 0.866 calculated in Chapter 2]. His calculations, based on median dates, indicate that peak food availability to the parents precedes the peak energy requirements of the chicks.

If adults consume 4796 kJ/day at the time of peak energy

availability (Butler 1991b) and have an estimated energy requirement of 1863 kJ, each parent, on average, could supply the nest with 2933 kJ/d. If peak energy demands of chicks (2027 kJ/d) occurs at the time of peak energy availability, parents would be able to provide for a total of 2.9 chicks. However, peak food availability to the parents precedes the peak energy requirements of the chicks (Butler 1991b). The mean number of young fledged per successful nest in British Columbia is 2.5 chicks (Forbes et al. 1985; Butler 1989). Sullivan (1988) hypothesized that adult herons can support a brood of three chicks under normal circumstances and that broods reduced to two chicks are probably the result of factors other than the provisioning ability of the parents.

The preceding calculations may not account for the energetic cost to the parents of travelling between the feeding and nesting sites. However, this is unlikely to be a major cost as nesting colonies are generally located within 5 km of the feeding areas (Thompson 1978; Dowd and Flake 1985, Butler 1991b) and adults often glide to conserve energy (H. de la Cueva and R. W. Butler, pers. com.). Breeding colonies are thought to be located near feeding areas in order to minimize the travelling cost to parents (Gibbs 1991).

Peak mortality of wild Great Blue Heron chicks generally occurs between 2 and 6 wk of age (Collazo 1981; Quinney 1982; Pratt and Winkler 1985; David and Berrill 1987; Butler 1989). This coincides with the peak energy requirements of the chicks

in this study (Fig. 3.2 and 3.3). As starvation is the primary cause of nestling mortality (Quinney 1982; Pratt and Winkler 1985), these observations support the hypothesis that reproductive success in Great Blue Herons is largely limited by the availability of food to the parents.

Sexual dimorphism

This study is the first to report sexual dimorphism in body mass for Great Blue Heron chicks. The asymptotic mass of male herons (2465 ± 51 g) was significantly greater ($P=0.001$) than the asymptotic mass of female herons (2179 ± 10 g). These values are similar to those previously reported for adult herons (Hartman 1961; Simpson 1984). The two sexes did not differ in their hatching mass, but by day 30 the male herons were significantly heavier than the female herons (Fig. 2.1). Quinney (1982) was not able to discern sexual dimorphism in growth of wild herons because his study ended when the birds were 28.5 d old.

There were no significant differences in EI_{ME} , nor in the energy requirements between male and female heron chicks in the present study. The small sample size (eight male and four female herons), large variability in EI_{ME} or differences in the components that make up E_{MAIN} , may have reduced the statistical power to detect sex differences in these parameters, particularly since the asymptotic mass of male heron chicks was only about 13 % greater than for females. Similarly, Collopy (1986) found no significant differences in food

consumption between captive male (n=2) and female (n=2) Golden Eagle (*Aquila chrysaetos*) chicks, although the asymptotic mass of female eagle chicks was about 16 % greater than for males.

Summary

This study provides evidence to support the hypothesis that reproductive success of Great Blue Herons is limited by the parents' ability to gather food (Powell 1983; Sullivan 1988). Brood size at fledging predicted by the relationship between parental effort (Butler 1991b) and the chicks' energy requirements (this study) is similar to the observed number of young fledged per successful nest (Forbes et al. 1985; Butler 1989). Peak mortality of nestlings (Collazo 1981; Quinney 1982; Pratt and Winkler 1985; David and Berrill 1987; Butler 1989) occur during the time of peak energy requirements of chicks (this study).

CHAPTER 4

**MAINTENANCE ENERGY REQUIREMENTS OF CAPTIVE
MALE GREAT BLUE HERONS (*ARDEA HERODIAS*)
IN RELATION TO ENVIRONMENTAL TEMPERATURE**

Introduction

Winter starvation is a common cause of mortality in northern populations of Great Blue Herons (*Ardea herodias*) (Butler 1991b), particularly during severe winters (Blus and Henny 1981). Juvenile herons (<12 month old) have higher rates of mortality than adult herons (Henny 1972; Butler 1991b) presumably because they are less efficient foragers than adult herons (Quinney and Smith 1980; Butler 1991b). First year survival rates of Grey Herons (*Ardea cinerea*) are related to winter weather conditions in Great Britain (North 1979; North and Morgan 1979).

No information is available on the energy requirements of Great Blue Herons during the winter. Calculation of the energy requirements of herons is particularly useful in understanding their winter mortality patterns. The objective of this study was to determine the maintenance energy requirements of captive Great Blue Herons in relation to environmental temperature.

Materials and Methods

Feeding trials were conducted on ten captive male Great Blue Herons [four juveniles in year 1 (August 1990-April 1991); four adults and six juveniles in year 2 (August 1991-February 1992)] during two fall and winter periods that differed in the severity of their winter months. The four birds tested in year 1 were tested again in year 2.

Herons were housed in outdoor aviaries (3.7 x 5 x 2.1 m pen in year 1 and 100 x 50 x 3 m pen in year 2) located at the South Campus Animal Facility, Department of Animal Science, University of British Columbia. Shelter from the wind and rain was provided. Herons were hand-fed fish (Table 4.1) 0-2 times per day. Water was provided *ad libitum*.

The minimum and maximum temperatures within the pen were recorded daily with a maximum-minimum thermometer. The daily mean temperature was calculated as the mean of the minimum and maximum temperatures of that day. Monthly mean temperature (T , °C) was calculated as the average of the daily mean temperatures for that month.

Nutritional analyses

Samples of fish were analyzed for energy, lipid and ash content as described in Chapter 2. Protein content of the fish was determined as the lean ash-free dry matter (100 % - % Lipid - % Ash).

Energy requirements

Herons were weighed individually to the nearest gram (Sartorius scale, model I 6800 A) each morning prior to feeding. The daily mass gain (g/d) was calculated as the difference between body mass (g) on consecutive days. Energy consumption was calculated as gross energy intake (EI_{GE}) rather than on the basis of metabolizable energy because the metabolizable energy coefficient (MEC) of herring was not reliable due to suspected oxidative rancidity of the herring

Table 4.1. Nutrient composition of fish fed to the Great Blue Herons
(*Ardea herodias*)^a.

Fish	n ^b	Dry Mass (% WM ^c)	Protein ^d (% DM ^c)	Lipid (% DM)	Ash (% DM)	Gross Energy (kJ/g DM)
Atlantic herring ^e	4	33.8±0.7	55.7±1.2	38.6±1.3	5.7±0.1	27.4±0.3
Pacific herring ^e	4	33.0±0.6	50.5±0.9	42.0±1.0	7.5±0.2	27.6±0.2
Mackerel ^e	4	29.1±0.5	76.8±2.7	16.4±3.0	6.8±0.4	22.7±0.5
Trout ^e	4	27.4±0.3	69.0±2.1	24.4±2.3	6.6±0.3	25.2±0.4
Trout ^f	- August	29.0±0.6	61.6±1.5	29.3±1.6	9.1±0.2	25.1±0.4
	- September	28.0±0.6	64.2±1.7	26.4±2.0	9.4±0.4	24.5±0.3
	- October	28.8±0.3	61.1±0.7	30.3±0.7	8.6±0.2	25.4±0.2
	- November	25.9±0.2	66.3±0.1	24.0±0.5	9.7±0.4	24.0±0.2
	- December	27.9±1.0	64.3±3.0	26.8±3.2	8.9±0.3	24.7±0.4
	- January	29.0±0.5	61.9±2.7	30.3±2.9	7.8±0.3	26.1±0.6
	- February	29.3±0.7	58.8±1.0	33.9±1.2	7.3±0.2	26.2±0.4

^aValues are given as means ± SEM.

^bEach sample is a pool of two fish.

^cWM = wet mass, DM = dry mass.

^d%Protein = 100 - %Lipid - %Ash.

^eFish fed in year 1.

^fFish fed in year 2.

used in that study (see Chapter 2).

Energy requirements of herons were determined using the method of Hurwitz *et al.* (1978) that is described in Chapter 3. Energy requirements of individual birds were determined for monthly periods between 1 August and 30 April in year 1 and between 1 August and 29 February in year 2. The type of body mass gain of individual herons was assumed to be homogeneous within each month.

Seasonal and temperature effects

Seasonal changes in body mass and EI_{GE} were estimated by calculating the mean body mass and EI_{GE} of individual herons for monthly periods. The effect of T on body mass, EI_{GE} and energy requirements were evaluated by determining the linear relationships between T and monthly averages of body mass, EI_{GE} and energy requirements. The lower critical temperature (T_{lc}) was defined as the T below which EI_{GE} and energy requirements increased significantly.

Statistical analyses

Statistical analyses were performed using SYSTAT 5.1 (Wilkinson 1990). Monthly differences were analyzed by analysis of variance followed by the Least Significant Difference test for means separation. Energy requirements and temperature effects were analyzed by linear regression. Data are reported as means \pm SEM.

Results

Monthly temperature

Monthly mean temperature within the heron pen decreased during the autumn, reached a nadir in December and January, and increased thereafter (February, March and April). This pattern was similar to the long-term monthly mean temperature recorded at the Vancouver International Airport (Environment Canada 1980) (Fig. 4.1). Year 2 was warmer than normal and year 1 was warmer than normal in most months except December when it was colder.

Body mass and energy intake

Body mass of the captive herons increased through the autumn months to a maximum in December of year 1 and January of year 2, and declined thereafter (Fig. 4.2A). Herons gained 641.0 ± 67.1 g in year 1 and 656.2 ± 66.7 g in year 2 between August and their peak winter mass. Monthly EI_{GE} of the herons was bimodal, with peaks in October and December of both years (Fig. 4.2B). The amplitude of these peaks differed between years. The EI_{GE} of October was significantly greater in year 2 than in year 1 ($P=0.004$), while EI_{GE} in December was significantly greater in year 1 than in year 2 ($P=0.002$).

A significant negative linear relationship was found between body mass and environmental T (Fig. 4.3A) ($P=0.001$, $R^2=0.57$). EI_{GE} was not significantly related to T above 7.9°C ($P=0.69$, $R^2=0.021$) and averaged 1416.2 ± 13.1 kJ/d (Fig. 4.3B). Below 7.9°C , a significant negative linear

Fig. 4.1. Mean daily environmental temperatures (means \pm SEM) observed in this study (year 1 O, year 2 ●). The long-term (1951-1980) mean daily temperature (■) recorded at the Vancouver International Airport (Environment Canada 1980) is provided for comparison.

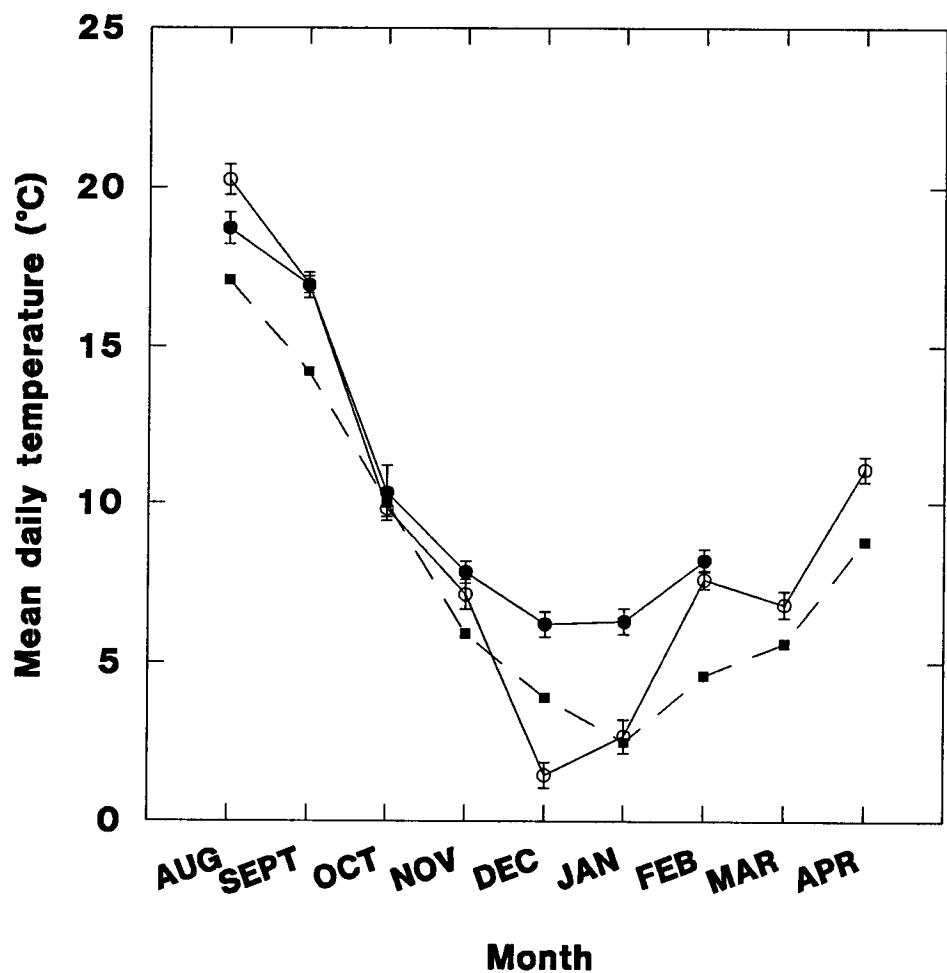


Fig. 4.2. Monthly body mass (A) and gross energy intakes (B) of captive male Great Blue Herons (*Ardea herodias*) (year 0, year 2 ●). Data are reported as means \pm SEM (year 1, n = 4; year 2, n = 10).

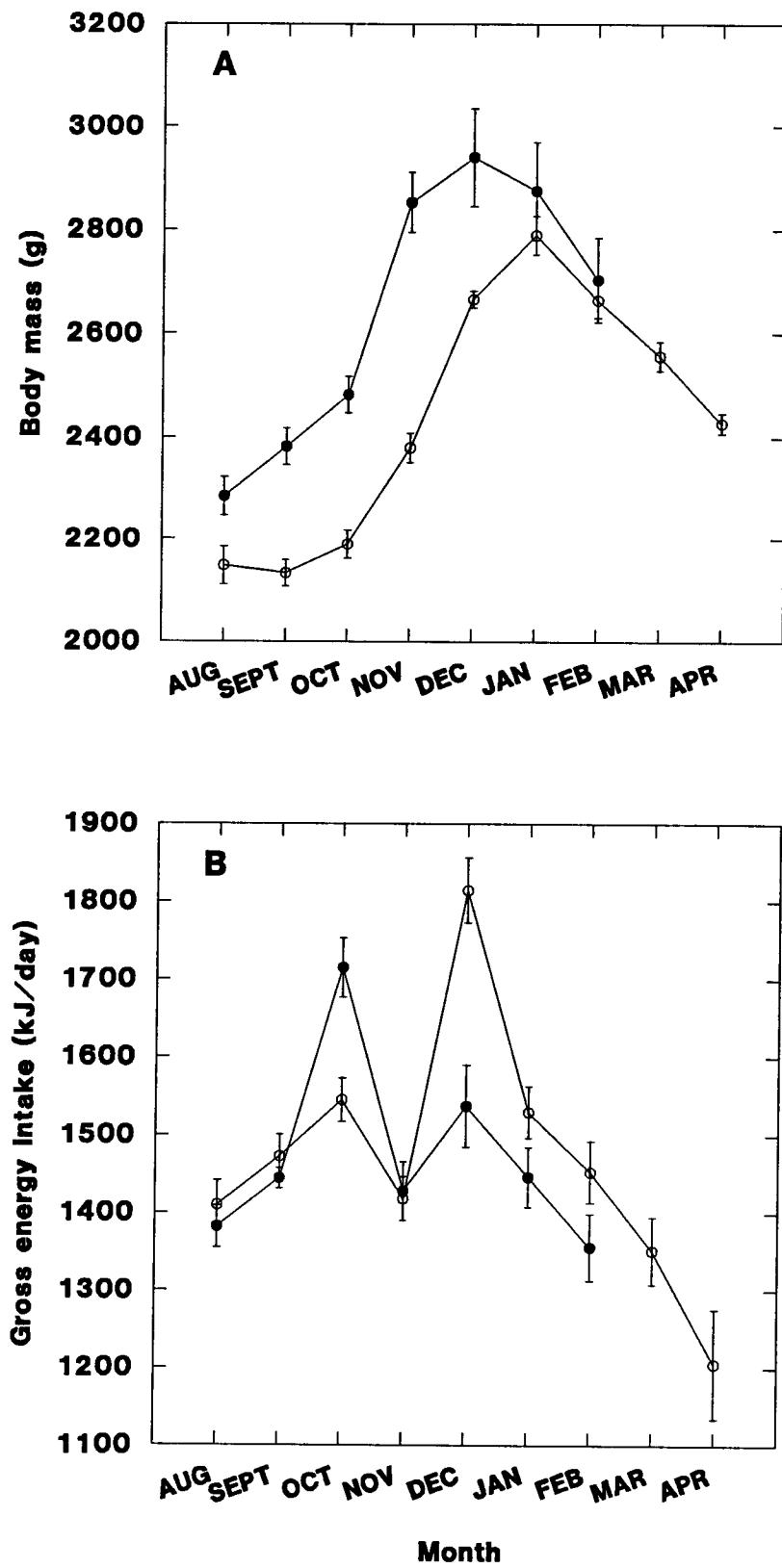
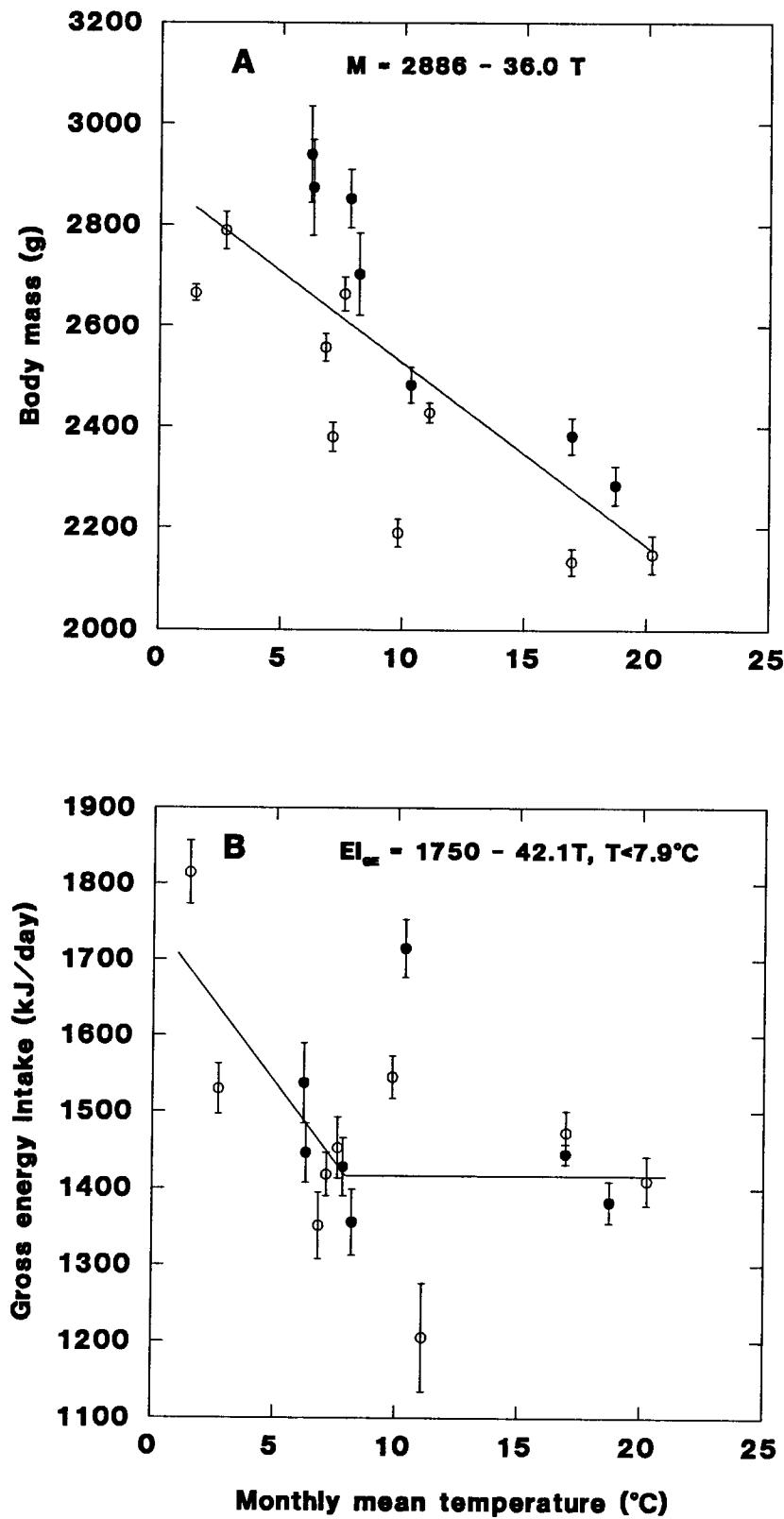


Fig. 4.3. The relationship between monthly averages of A) body mass (M) and B) gross energy intake (EI_{GE}) of captive male Great Blue Herons (*Ardea herodias*) with monthly mean temperature (year 1 O, year 2 ●). Data are reported as means \pm SEM (year 1, n = 4; year 2, n = 10).



relationship was found between EI_{GE} and T ($P<0.006$, $R^2=0.58$) (Fig. 4.3B). This corresponds to the period of November to March in normal years (Fig. 4.1). EI_{GE} in October of year 2 was greater than that predicted by this relationship (Fig. 4.3B), and presumably represents a short term response to unseasonable temperatures as mean daily temperature decreased significantly ($P<0.001$) from $12.3 \pm 0.9^\circ\text{C}$ during the first 22 d of this month to $5.4 \pm 0.7^\circ\text{C}$ during the last 9 d of the month. Consequently, October of year 2 was excluded from the calculation for the effects of temperature on EI_{GE} and energy requirements.

Energy requirements

The energy requirement for maintenance (E_{MAIN}) and gain (E_{GAIN}) varied significantly among months ($P<0.001$ and $P=0.02$, respectively) (Fig. 4.4). E_{MAIN} was significantly related to T (Fig. 4.5A). Between 9.6°C and 20.2°C , E_{MAIN} and T were positively related ($P=0.004$, $R^2=0.77$), while below 9.6°C they were negatively related ($P=0.004$, $R^2=0.63$) (Fig. 4.5A). E_{GAIN} was not significantly related to T ($P=0.078$, $R^2=0.21$) and averaged 16.44 kJ/g gain throughout the experimental period (Fig. 4.4B).

Total maintenance energy requirements were calculated on a whole bird basis (kJ/bird/d) by multiplying E_{MAIN} ($\text{kJ/g}^{0.67}/\text{d}$) by the metabolic body mass ($M^{0.67}$, $\text{g}^{0.67}$) for each month (ie. $E_{MAIN} \times M^{0.67}$). Total maintenance energy requirements did not change between monthly mean temperatures of 7.6 and 20.2°C ($P=0.91$,

Fig. 4.4. Monthly energy requirements for A) maintenance (E_{MAIN}) and B) gain (E_{GAIN}) of captive male Great Blue Herons (*Ardea herodias*) (year 1 ○, year 2 ●). Data are reported as means \pm SEM (year 1, n = 4; year 2, n = 10).

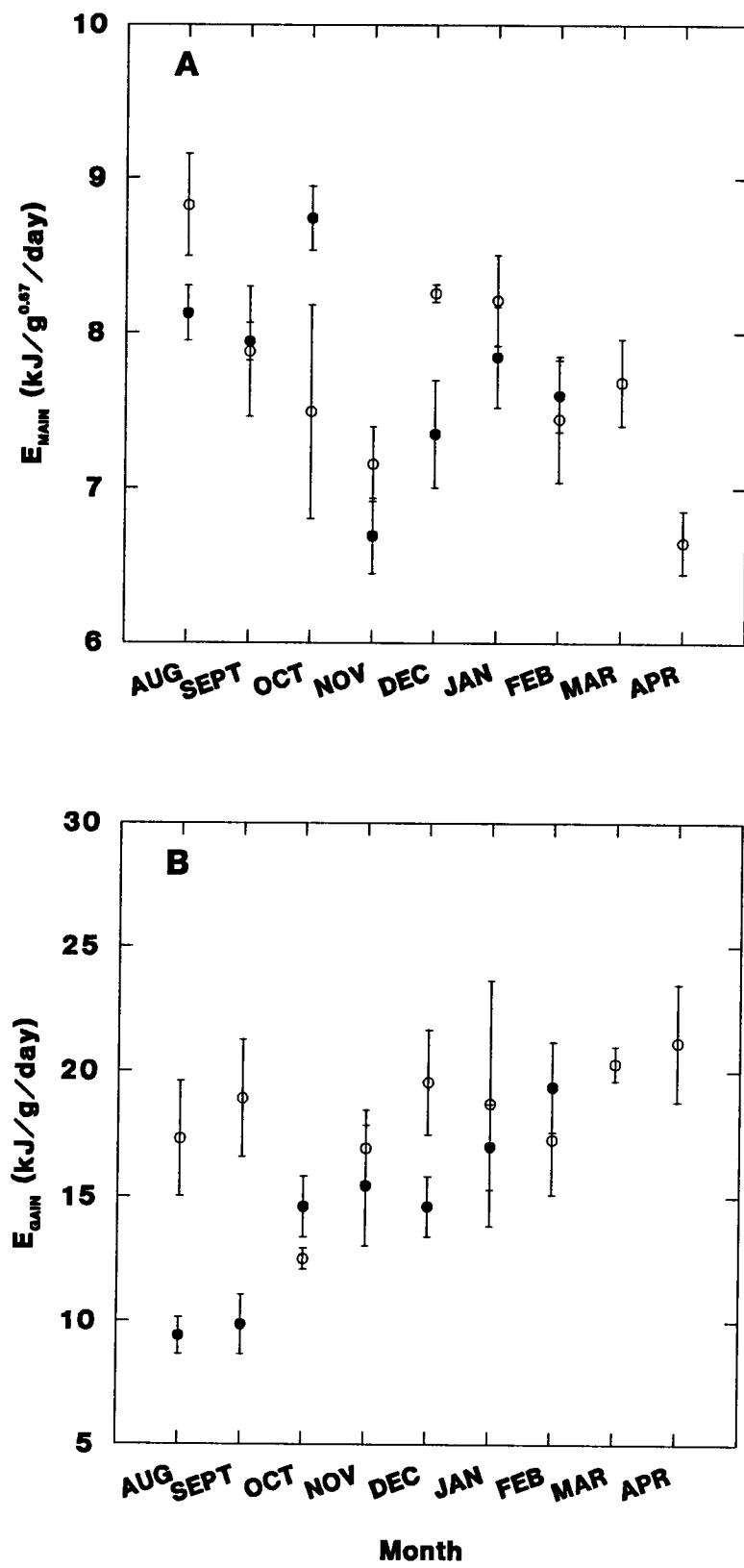
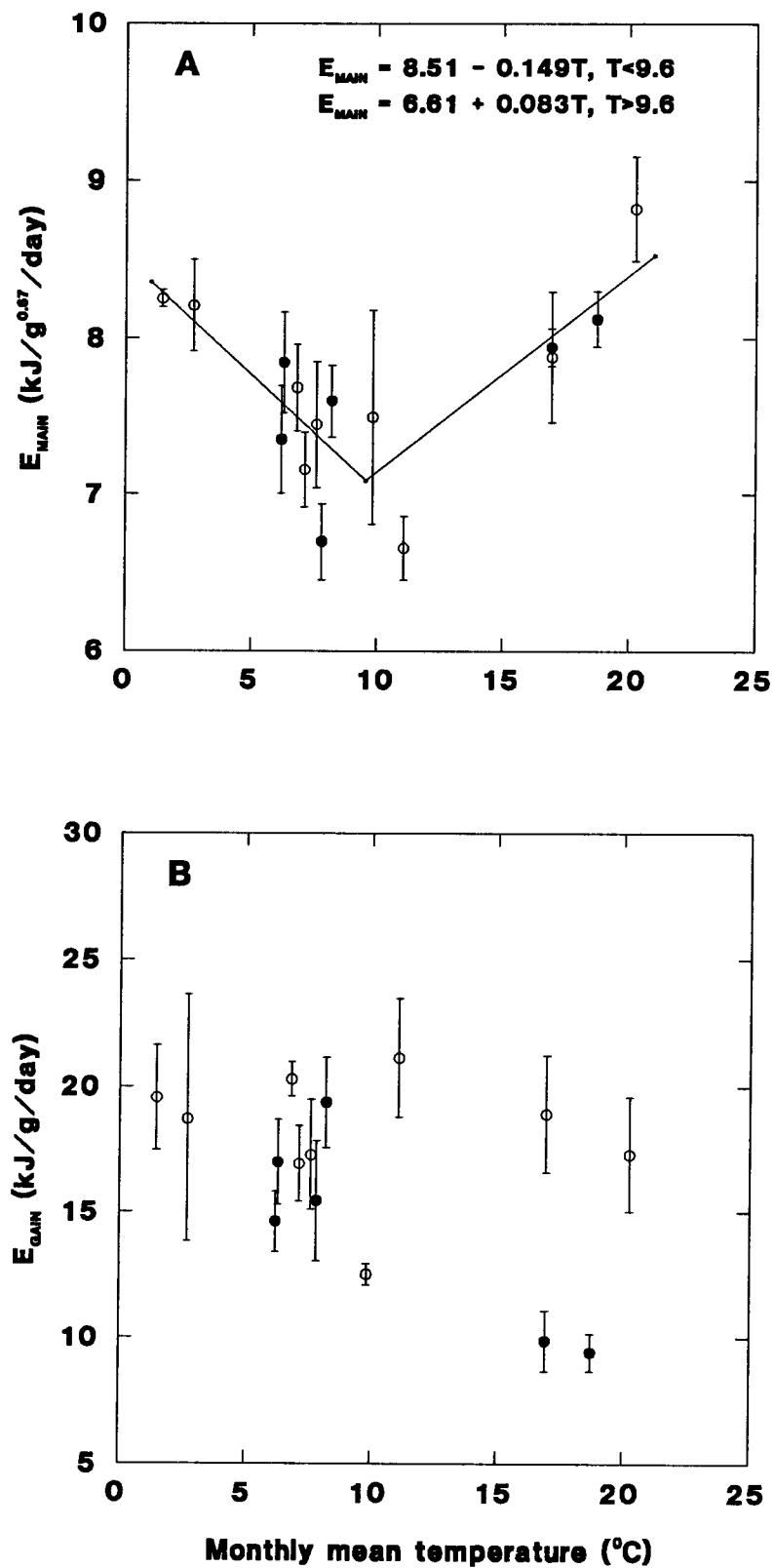


Fig. 4.5. The relationship between the energy requirements for A) maintenance (E_{MAIN}) and B) gain (E_{GAIN}) of captive male Great Blue Herons (*Ardea herodias*) with monthly mean temperature (year 1 ○, year 2 ●). Data are reported as means \pm SEM (year 1, n = 4; year 2, n = 10).



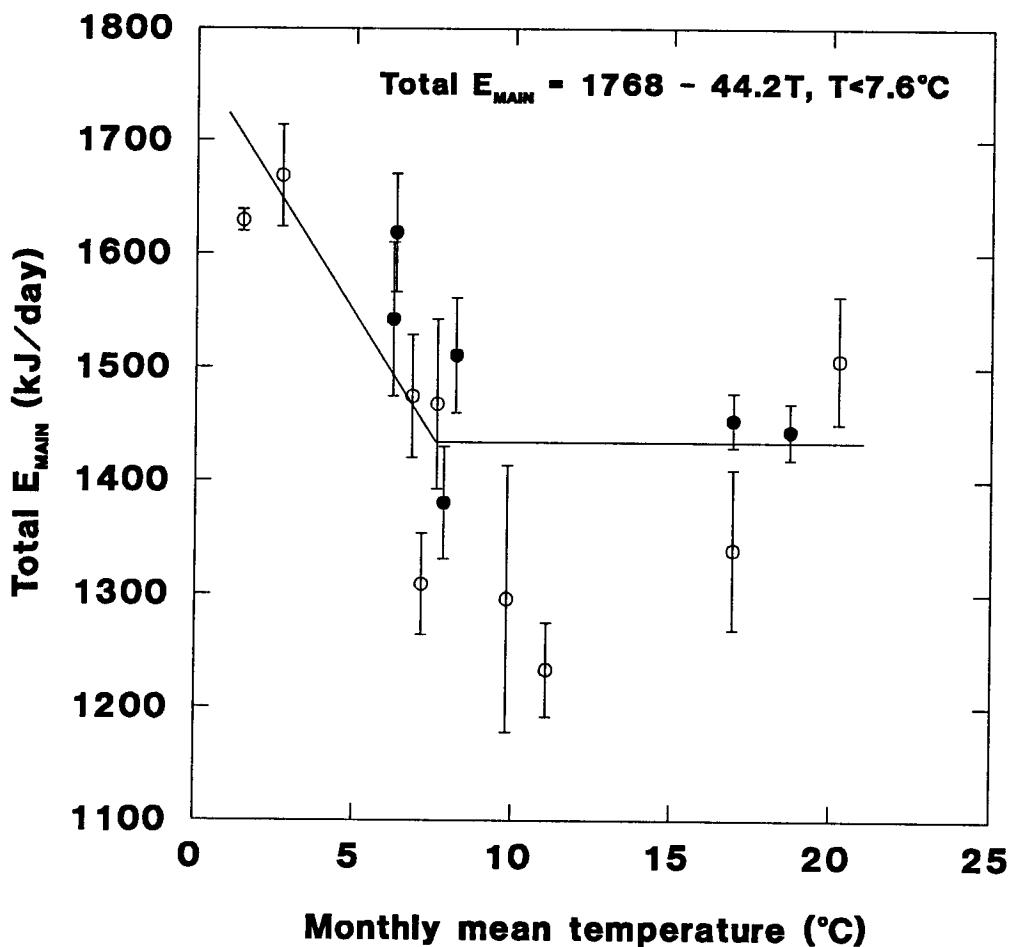
$R^2=0.02$) and averaged $1434.1 \pm 34.6\text{ kJ/d}$. Below 7.6°C , a significant negative linear relationship was found between the total maintenance energy requirement and T ($P=0.001$, $R^2=0.71$) (Fig. 4.6).

Discussion

This study is the first to report seasonal changes in body mass for Great Blue Herons. Body mass increased through the autumn months to a maximum in early winter and declined during late winter (Fig. 4.2A). This pattern of seasonal changes in body mass has been reported in many species of captive and wild wintering birds (Dugan et al. 1981; Ankney 1982; Reinecke et al. 1982; Coulson et al. 1983; Hepp 1986; Perry et al. 1986; Lehikoinen 1987; Ely and Raveling 1989; Rodgers and Rodgers 1990) and reflects changes in lipid and protein stores (endogenous reserves) (King 1972; Reinecke et al. 1982; Ely and Raveling 1989). Increased endogenous reserves are thought to supply an emergency energy reserve during periods of food shortage or severe weather (Blem 1990; above references). The decline in body mass in late winter may represent a change in the relative advantages of maintaining endogenous energy reserves and the cost of carrying extra mass (Reinecke et al. 1982).

EI_{GE} of captive herons in this study varied seasonally (Fig. 4.2B) and were significantly related to T (Fig. 4.3B). The lower critical temperature below which EI_{GE} increased was

Fig. 4.6. The relationship between the total maintenance energy requirement (Total E_{MAIN}) of captive male Great Blue Herons (*Ardea herodias*) with monthly mean temperature (year 1 ○, year 2 ●). Data are reported as means \pm SEM (year 1, n = 4; year 2, n = 10).



7.9°C (Fig. 4.3B). EI_{GE} of the herons in April of year 1 and October of year 2 were different from the predicted EI_{GE} . The low EI_{GE} in April of year 1 was probably due to the combination of warm temperatures ($T > T_{lc}$) and the utilization of endogenous reserves (birds were losing body mass). The high EI_{GE} in October of year 2 presumably represents a short term response to unseasonably low temperatures (see Results). These results suggest that Great Blue Herons respond to both short and long term declines in air temperature.

Changes in E_{MAIN} (Fig. 4.5) were presumably due to changes in the amount of energy allocated to components that are included in maintenance costs: basal metabolism, heat increment of feeding, thermoregulation and voluntary activity (Harris 1966; Ricklefs 1974; Kendeigh et al. 1977). However, seasonal changes in E_{MAIN} are complicated by seasonal changes in body composition (winter fattening). The addition of largely inert adipose tissue could distort mass-independent E_{MAIN} calculations. To overcome this problem, maintenance energy requirements were calculated on a whole bird basis [by multiplying the mass-independent E_{MAIN} by the bird's metabolic body mass ($M^{0.67}$)]. The relationship between total (or whole bird) maintenance energy requirements and T (Fig. 4.6) was similar to the relationship between EI_{GE} and T (Fig. 4.3B). Total maintenance energy requirements did not change above the T_{lc} , and increased in a linear fashion below T_{lc} (Fig. 4.6).

The lower critical temperatures for EI_{GE} and total

maintenance energy requirements were 7.9°C (Fig. 4.3) and 7.6°C (Fig. 4.6), respectively. Therefore, for T below about 8°C, herons have increased energy requirements and must obtain more food in order to fulfil these increased energy requirements. Monthly mean temperature declined to and below T_{lc} in November in the herons' pen, and, presumably in the rest of southwestern British Columbia (Fig. 4.1). At this time, wild juvenile and adult female herons in the Fraser River Delta of British Columbia move into adjacent grasslands and estuarine marshes because high tides and declining fish populations make foraging unprofitable on the beaches (Butler 1991b). Therefore, herons wintering in coastal British Columbia are faced not only with increased thermoregulatory costs, but also declining prey availability.

Endogenous reserves are thought to supply an emergency energy reserve for birds during periods of food shortage or severe weather (Blem 1990). Captive herons in the present study gained approximately 650 g between August and the time of peak winter mass (Fig. 4.2A) with an average E_{GAIN} of 16.44 kJ/g (gross energy basis). Assuming herons metabolize 86.6 % of the gross energy in fish diets (Chapter 2), the metabolizable E_{GAIN} would be 14.24 kJ/g ($16.44 \text{ kJ/g} \times 0.866$). Assuming that tissue catabolism would yield 14.24 kJ/g (ie. tissue catabolism as 100% efficient), 650 g of body mass represents 9260 kJ ($650 \text{ g} \times 14.24 \text{ kJ/g}$) of energy reserve for the heron. The total metabolizable energy requirement for

maintenance at 0°C is 1530 kJ/d [calculated from the gross energy requirement predicted in Fig. 4.5 (1768 kJ/d) and assuming MEC = 0.866]. Therefore, at 0°C this reserve could potentially meet a heron's total maintenance energy requirements for approximately 6 d if food was not available. Herons require some energy to fly to foraging areas and roost sites so this estimate of 6 d is likely high.

Herons that die of starvation during the winter in British Columbia weigh approximately 500 g below the baseline (August) body mass of male herons seen in this study (R.W. Butler, pers. com.). Assuming tissue catabolism yields 14.24 kJ/g and the total metabolizable energy requirement for maintenance at 0°C is 1530 kJ/d, catabolism of this 500 g of body tissue could supply the heron's energy needs for 4.7 d. If wild Great Blue Herons follow a similar pattern of seasonal changes in body mass as seen in this study, the peak winter body mass of herons could represent a potential energy reserve of 10.7 d (6 d energy reserve + 4.7 d marginal reserve). These calculations do not take into account adverse weather conditions due to wind and precipitation, which would increase maintenance energy requirements and thereby exhaust energy reserves at a faster rate. Body mass of wintering birds has been shown to be positively correlated to survival (Coulson et al. 1983; Haramis et al. 1986).

The above calculations only apply to adult herons, as juvenile herons wintering on the Fraser River Delta in British

Columbia in good condition weigh approximately 2210 g (R.W. Butler, pers. com.). At best, it appears that juvenile herons are able to obtain enough food to meet maintenance energy requirements but not to build endogenous reserves. Juvenile herons are less efficient foragers than adults (Quinney and Smith 1980; Butler 1991b) and do not maintain feeding territories (Butler 1991b). The consequences of poor foraging ability, low food availability and high maintenance energy requirements likely contribute to the high mortality of juvenile herons during the winter months in south-western British Columbia.

Chapter 5
General Discussion

Food limitations are important determinants of life-history traits in birds through their effects on reproductive success and survival (reviewed by Martin 1987). Knowledge of energy requirements is therefore important in understanding a bird's life-history pattern. The objective of the research in this thesis was to determine the energy requirements of Great Blue Herons (*Ardea herodias*) during critical stages of their life-history when food is considered limiting (ie. as chicks and during the winter).

A continuous feeding trial was used to determine the energy requirements of hand-reared Great Blue Heron chicks (Chapter 3). Daily metabolizable energy intake (EI_{ME}) increased with age up to 26 d, remained relatively constant at 2027 ± 25 kJ for the next 16 d (26 to 41 d) and decreased to 1545 ± 22 kJ by day 50 (Fig. 3.2). Chick energy requirements followed a similar pattern (Fig. 3.3). Total energy requirements and total energy required for maintenance increased to a maximum between 30 and 39 d of age and declined thereafter. Total energy required for gain was greatest between 10 and 29 d of age, the time of maximum growth.

These energy requirements are significant with regard to their relationship to parental effort and to chick mortality. Brood size at fledging predicted by the relationship between parental effort (Butler 1991) and the chicks' energy requirement (this study) is similar to the observed number of young fledged per successful nest (Forbes et al. 1985; Butler

1989). Peak mortality of nestlings (Collazo 1981; Quinney 1982; Pratt and Winkler 1985; David and Berrill 1987; Butler 1989) coincides with the age of peak energy requirements of chicks determined in this study.

Asynchronous hatching is often viewed as a parental strategy to deal with an unpredictable food supply (Lack 1954). By creating a size hierarchy (and therefore competitive asymmetries), parents may facilitate adaptive brood reduction and thus secondarily adjust brood size to the prevailing food supply (Lack 1954). The relationships outlined above support the brood reduction hypothesis for Great Blue Herons.

Adult male herons are heavier than adult female herons (Hartman 1961; Simpson 1984). Prior to this study it was not known at what age herons became sexually dimorphic. The two sexes did not differ in their hatching mass in this study, but by day 30 male chicks were significantly heavier than female chicks (Fig 2.1). Male chicks at fledging were about 13 % heavier than female chicks (2465 and 2179 g, respectively). Although no significant differences in EI_{ME} and energy requirements were found between the sexes, sex may influence dominance patterns and hence, food distribution within the brood. If by chance the older chicks are male and the younger chicks are female, male chicks should be able to maintain their dominance throughout chick rearing due to their larger size. However, if the older chicks are female and the younger

chicks are male, female chicks may not be able to maintain their dominance once the male chicks become larger. Evidence contrary to this possibility was provided by Drummond *et al.* (1991) who showed that older chicks remain dominant, regardless of sex, in sexually dimorphic Blue-footed Boobies.

Mock (1985, 1987) related sibling aggression (and hence brood reduction) to the size of the food delivered to the nest by parents. Dominant chicks could monopolize small food items but not items too large to seize and swallow. Recently, Anderson *et al.* (1993) tested the hypothesis that prey size determines the extent to which sexual size dimorphism influences sibling competition in kestrels (female kestrels are larger than male kestrels). When parents delivered small monopolizable food items, female chicks outcompeted their male siblings. When parents delivered larger, unmonopolizable food items, competitive ability and sex were unrelated. Sexual dimorphism and sibling competition in herons remains to be investigated.

A continuous feeding trial was used to determine the maintenance energy requirements of Great Blue Herons in relation to winter temperature (Chapter 4). The lower critical temperatures for energy intake and total maintenance energy requirements of the captive herons were 7.9°C (Fig. 4.3) and 7.6°C (Fig. 4.6), respectively. Therefore, for monthly mean temperature below about 8°C, herons have increased energy requirements and must obtain more food to

satisfy those energy requirements.

This study was the first to report seasonal changes in body mass for Great Blue Herons. Body mass increased through the autumn months to a maximum in early winter and declined during late winter (Fig. 4.2A). Seasonal changes in body mass reflect changes in endogenous reserves (King 1972; Reinecke et al. 1982; Mortensen et al. 1983; Ely and Raveling 1989), which are thought to be emergency energy reserves for periods of food shortage or severe weather (Blem 1990). The captive herons in the present study gained about 650 g between August and the time of peak winter mass. This reserve could potentially meet a heron's total maintenance energy requirements for approximately 6 d at 0°C if food was not available. The 500 g "marginal reserve" (R.W Butler, pers. com.) could potentially meet a heron's total maintenance energy requirements for 4.7 d at 0°C if food was not available. If wild herons follow a similar pattern of seasonal changes in body mass as those seen in this study, the peak winter body mass could represent a potential energy reserve of 10.7 d (6 d reserve + 4.7 d marginal reserve). However, juvenile herons, at best, are only able to obtain enough food to meet maintenance energy and not to build endogenous reserves. The high mortality of juvenile herons during the winter is likely the consequences of poor foraging ability (Quinney and Smith 1980; Butler 1991), low food availability (Butler 1991) and high maintenance energy

requirements (this study).

Endogenous reserves play an important role in avian reproduction. Many species of waterfowl use endogenous reserves to meet the demands of laying and incubating eggs (Ankney and MacInnes 1978; Raveling 1979; Krapu 1981; Drobney 1982; Ankney and Afton 1988; Afton and Ankney 1991; others). The extent to which female herons use endogenous reserves for egg production is not known. Butler (1991b) found that many female herons began to lay eggs several days after energy consumption crossed an estimated energy threshold for egg laying, possibly due to variations in body condition (endogenous reserves).

Parents may rely, in part, on endogenous reserves to meet their energy needs during chick rearing. As parents become increasingly food limited due to lessened endogenous reserves, they must acquire more exogenous energy for themselves, and consequently devote less energy to chicks (Martin 1987). The importance of endogenous reserves to breeding herons remains to be investigated.

Conclusion

The findings in this thesis provide evidence that point to the importance of energy limitation as determinants of life-history traits in herons.

In this thesis, I determined that:

- 1) Great Blue Herons metabolize 86.6 % of the energy in fish diets (Chapter 2).

- 2) The growth of hand-reared Great Blue Heron chicks is similar to that predicted for a heron species fledging at 2.3 kg (Chapter 3). Sexual dimorphism in body mass become apparent at 30 d of age, however, no differences in EI_{ME} nor in energy requirements between the sexes were detected. EI_{ME} of chicks was maximum between days 26 and 41 at $2027 \pm 25 \text{ kJ/d}$.
- 3) The lower critical temperature below which energy intake and maintenance energy requirements of captive male Great Blue Herons increase are 7.9°C and 7.6°C , respectively (Chapter 4). Body mass of the captive herons changed seasonally, presumably representing changes in endogenous reserves.

Future directions

Future work might consider the following issues raised in this thesis: 1) the relationship between sex and brood reduction in herons, 2) reproductive costs to parents, and 3) seasonal changes in body mass and body composition of herons in relation to survival.

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Appendix 1. Glossary of abbreviations.

Symbol	Name	Units
A	Asymptotic mass	g
ADE	Apparent digestible energy	kJ
AGR	Absolute growth rate	g/day
AME	Apparent metabolizable energy	kJ
AMEC	Apparent metabolizable energy coefficient	
AMEC _n	Nitrogen corrected AMEC	
E _{MAIN}	Energy requirement for maintenance	kJ/g ^{0.67} /day
E _{GAIN}	Energy requirement for gain	kJ/g/day
E _{TOT}	Total energy requirement	kJ/day
EI	Voluntary energy intake	kJ/day
EI _{GE}	Voluntary gross energy intake	kJ/day
EI _{ME}	Voluntary metabolizable energy intake	kJ/day
FE	Faecal energy	kJ
FE _n	Nitrogen corrected FE	kJ
F _i E	Faecal energy energy of food origin	kJ
F _m E	Metabolic faecal energy	kJ
F _m E _n	Nitrogen corrected F _m E	kJ
FN	Faecal nitrogen	g
G	Mass gain	g/day
GE	Gross energy	kJ

Appendix 1. Glossary of abbreviations (continued).

Symbol	Name	Units
HI	Heat increment of feeding	kJ
i	Hatching mass	g
IE	Ingested energy	kJ
IN	Ingested nitrogen	g
k	Logistic growth rate	day ⁻¹
M	Mass	g
M ^{0.67}	Metabolic mass	g ^{0.67}
ME	Metabolizable energy	kJ
ME _{MAIN}	Metabolizable energy for maintenance	kJ
ME _{PROD}	Metabolizable energy for production	kJ
NE	Net energy	kJ
NE _{MAIN}	Net energy for maintenance	kJ
NE _{PROD}	Net energy for production	kJ
RN	Retained nitrogen	g
t	Age	days
T	Mean monthly temperature	°C
T _{lc}	Lower critical temperature	°C
TDE	True digestible energy	kJ
TME	True metabolizable energy	kJ
TMEC	True metabolizable energy coefficient	
TMEC _n	Nitrogen corrected TMEC	

Appendix 1. Glossary of abbreviations (continued).

Symbol	Name	Units
UE	Urinary energy	kJ
UE _n	Nitrogen corrected UE	kJ
U _f E	Urinary energy of food origin	kJ
U _e E	Endogenous urinary energy	kJ
U _e E _n	Nitrogen corrected U _e E	kJ
UN	Urinary nitrogen	g

Appendix 2. Growth rate and asymptotic mass of various species of herons.

Species	Growth rate		Asymptotic mass (g)	Source
	k ^a (day ⁻¹)	AGR ^b (g/day)		
<i>Ardea cinerea</i>	0.257	55.0	1402	Owen 1960
<i>A. herodias</i>	0.173	65.6	2340	This study
<i>A. goliath</i>	0.121	89.8	4500	Junor 1972
<i>A. purpurea</i>	0.196	38.2	1150	Tomlinson 1975
<i>Bubulcus ibis</i>	0.272	14.6	360	Siegfried 1972
<i>Butorides striatus</i>	0.294	8.4	175	Gavino and Dickerman 1972
<i>Cochlearius cochlearius</i>	0.202	13.8	330	Juarez and Dickerman 1972
<i>Egretta alba</i>	0.163	24.2	732	Tomlinson 1976
<i>E. caerulea</i>	0.265	14.8	279	Werschkul 1979
<i>E. thula</i>	0.263	11.0	206	St. Clair Raye and Burger 1979
<i>Ixobrychus minutus</i>	0.311	6.1	130	Langley 1983
<i>Nycticorax nycticorax</i>	0.264	26.8	683	Wolford and Boag 1971
<i>N. leuconotus</i>	0.174	16.1	420	Junor 1972