

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

DARIN C. BENNETT,¹ PHILIP E. WHITEHEAD,² AND LESLIE E. HART¹

¹Department of Animal Science, University of British Columbia,
Vancouver, British Columbia V6T 1Z4, Canada; and

²Canadian Wildlife Service, P.O. Box 340, Delta, British Columbia V4K 3Y3, Canada

ABSTRACT.—The energy requirements of 12 hand-reared Great Blue Heron (*Ardea herodias*) chicks were determined using a continuous feeding trial. 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. At fledging, male chicks ($\bar{x} = 2,465 \pm$ SE of 51 g) were about 13% heavier than female chicks ($2,179 \pm 10$ g). The growth rate of male chicks (logistic growth rate [k] of 0.167 ± 0.004 /day and absolute growth rate [AGR] of 70.7 ± 4.1 g/day) was significantly different from the growth rate of female chicks (k of 0.178 ± 0.003 /day, and AGR of 60.5 ± 0.4 g/day). Metabolizable energy intake (El_{ME}) and energy requirements did not differ between male and female chicks. El_{ME} was maximal between days 26 and 41 at $2,027 \pm 25$ kJ/day. The total energy requirement for gain (kJ/day) was greatest between 10 and 29 days of age, the time of maximum growth. The total energy requirement for maintenance (kJ/day) was greatest between 30 and 39 days of age. Our study provides evidence to support the hypothesis that reproductive success of Great Blue Herons is limited by the parents' ability to gather food. Brood size at fledging predicted by the relationship between parental effort and the chicks' energy requirements is similar to the observed number of young fledged per successful nest. Peak mortality of wild nestlings occurs during the time of peak chick energy requirements as indicated by our study. Received 7 June 1993, accepted 24 October 1993.

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 evaluate fully energy limitations on reproductive success. Little is known about energy requirements of Great Blue Heron chicks except that the peak number of feeding visits by parents occurs at about 29 days after hatching (Dowd and Flake 1985) and parents ingest more energy when feeding small chicks than large chicks (Butler 1993).

Quinney (1982) found body mass of wild Great Blue Heron chicks during the first month of life increased in a nearly linear manner, and no discernible sexual dimorphism was observed

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

MATERIALS AND METHODS

Animals and rearing procedures.—Eggs were collected from three Great Blue Heron colonies in southwestern 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 × 16.5 × 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

TABLE 1. Nutrient composition of fish fed to the Great Blue Heron chicks.^a

Fish	n ^b	Dry mass (% WM)	Lipid (% DM)	Ash (% DM)	Protein ^c (% DM)	Gross 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

^a $\bar{x} \pm SE$; WM = wet mass, DM = dry mass.

^b Each sample is pool of two fish.

^c % protein = 100% - (% lipid) - (% ash).

temperature accordingly. Chicks were transferred to wood-framed nest boxes when they were two to three weeks 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 × 50 × 3 m) when the youngest chick was older than 50 days of age, corresponding to the age when heron chicks climb out of nests onto tree limbs (Butler 1989). Blood samples were taken from heron chicks and sent to Zoogen Inc. (Davis, California) for sex determination by restriction-fragment-length-polymorphism analysis.

Chicks were hand-fed salmonids (*Oncorhynchus* spp.; Table 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 to 5, 6 to 10, and 11 to 75 days 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 dried at 60°C for 7 to 14 days until mass was constant. Dried fish samples were ground individually and homogenized in a coffee grinder. Subsamples of the fish were used to determine energy content by bomb calorimetry (Leco Automatic Calorimeter model AC-300, Leco Corporation, St. Joseph, Michigan) standardized with benzoic acid. A second subsample was used to measure lipid content following Goldfish extraction (Labconco Corporation, Kansas City, Missouri) with diethyl ether as a solvent. A third subsample was ashed at 600°C in a muffle furnace for 24 h. 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 g (Sartorius scale, model I 6800 A) each day prior to the first feeding. The relationship between chick mass (M , grams) and age (t , days) was described using the logistic equation:

$$M = A / (1 + be^{-kt}), \quad (1)$$

where b is $(A - i)/i$, A is the asymptotic mass, i is the hatching mass, and k is the logistic growth rate (per day; Ricklefs 1983). The daily mass gain (G , grams/day) was calculated as the difference between the mass on consecutive days. The absolute growth rate (AGR,

grams/day) was calculated as the average daily mass gain during the linear period of growth (Drent and Daan 1980).

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 percent dry matter and gross energy content of the fish (Table 1). Adult herons, on average, metabolize 86.6% of the energy in fish diets (Bennett and Hart 1993). The metabolizable energy intake (El_{ME} , kJ/day) of the heron chicks was calculated by multiplying the gross energy intake by a true metabolizable energy coefficient (MEC) of 0.866. Our assumption that the chicks were as efficient as adults was based on previous findings that there were no differences in metabolizable energy among chickens of various ages (Sibbald 1978, Shires et al. 1980).

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/day) 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 (i.e. within a measurement period; Hurwitz et al. 1978). The model is expressed as

$$E_{TOT} = E_{MAIN}M^{0.67} + E_{GAIN}G, \quad (2)$$

which can be linearized to

$$E_{TOT}/G = (E_{MAIN}M^{0.67}/G) + E_{GAIN}, \quad (3)$$

where E_{MAIN} is estimated by the slope of the regression of E_{TOT}/G on $M^{0.67}/G$ and is expressed as kJ per gram metabolic body mass in a day ($\text{kg g}^{-0.67} \text{day}^{-1}$), and E_{GAIN} is estimated by the intercept of this regression and is expressed as kJ per gram metabolic body mass gain in a day ($\text{kg g}^{-1} \text{day}^{-1}$). El_{ME} was substituted into equation 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 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 unpubl. 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 days. For each 10-day 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 (i.e. $M^{0.67}E_{\text{MAIN}}$ and GE_{GAIN} , respectively). Since herons, on average, metabolize 86.6% of the gross energy in fish diets (Bennett and Hart 1993), excreta losses were assumed to account for 13.4% of the gross energy intake of the chicks.

Statistical analyses.—Statistical analyses were performed using SYSTAT 5.1 (Wilkinson 1990). The logistic equation (eq. 1) was fit by nonlinear estimation, while Hurwitz's equation (eq. 3) was fit by linear regression. Sex differences in body mass, El_{ME} , and growth rates were analyzed by *t*-tests. Sex and developmental differences in energy requirements were analyzed by the following statistical model:

$$Y_{ij} = \mu + S_i + P_j + (SP)_{ij} + e_{ij} \quad (4)$$

for *i* of 1 and 2, and *j* of 1 through 6, where Y_{ij} is the energy requirement for maintenance or gain, S_i is the sex of the chick, P_j is the developmental period, $(SP)_{ij}$ is the interaction between sex and period, and e_{ij} is the error term. The least-significant-difference test was used to evaluate differences in means, (Wilkinson 1990). If no sex differences were found, data from all 12 birds were pooled. Data are reported as $\bar{x} \pm \text{SE}$.

RESULTS

Growth.—The hatching mass of male herons (54.2 ± 1.6 g; $n = 8$) was not significantly different ($P = 0.41$) from that of female herons (52.6 ± 0.9 g; $n = 4$). However, the asymptotic masses, as determined by logistic curves, were about 13% greater for male chicks ($2,465 \pm 51$ g) than for female chicks ($2,179 \pm 10$ g), and this difference was significant ($P = 0.001$; Fig. 1). As expected, the growth rate of male herons ($k = 0.167 \pm 0.004/\text{day}$ and $\text{AGR} = 70.7 \pm 4.1$ g/day) was significantly different (k , $P = 0.03$; AGR , $P < 0.001$) from the growth rate of female herons ($k = 0.178 \pm 0.003/\text{day}$ and $\text{AGR} = 60.5 \pm 0.4$ g/day). Both sexes reached their asymptotic mass by 60 days of age (Fig. 1).

Energy requirements.—Daily El_{ME} increased with

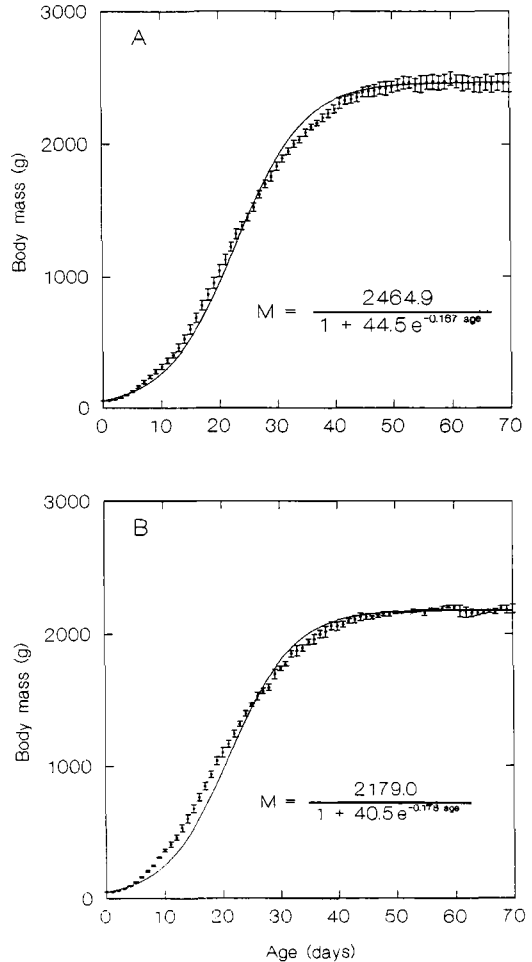


Fig. 1. Body mass ($\bar{x} \pm \text{SE}$) of (A) male ($n = 8$) and (B) female ($n = 4$) hand-reared Great Blue Heron chicks as a function of age. Solid lines represent growth curves described by logistic equations.

age up to day 26, remained relatively constant at $2,027 \pm 25$ kJ for the next 16 days (days 26 to 41) and decreased to $1,545 \pm 22$ kJ by day 50 (Fig. 2). Daily El_{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 0.74 , respectively). Both E_{MAIN} and E_{GAIN} varied significantly among developmental periods ($P = 0.004$ and 0.032 , respectively), but not between males and females ($P = 0.56$ and 0.61 , respectively). Energy requirements are listed in Table 2.

Energy budgets of male and female heron chicks followed similar patterns (Table 3, Fig.

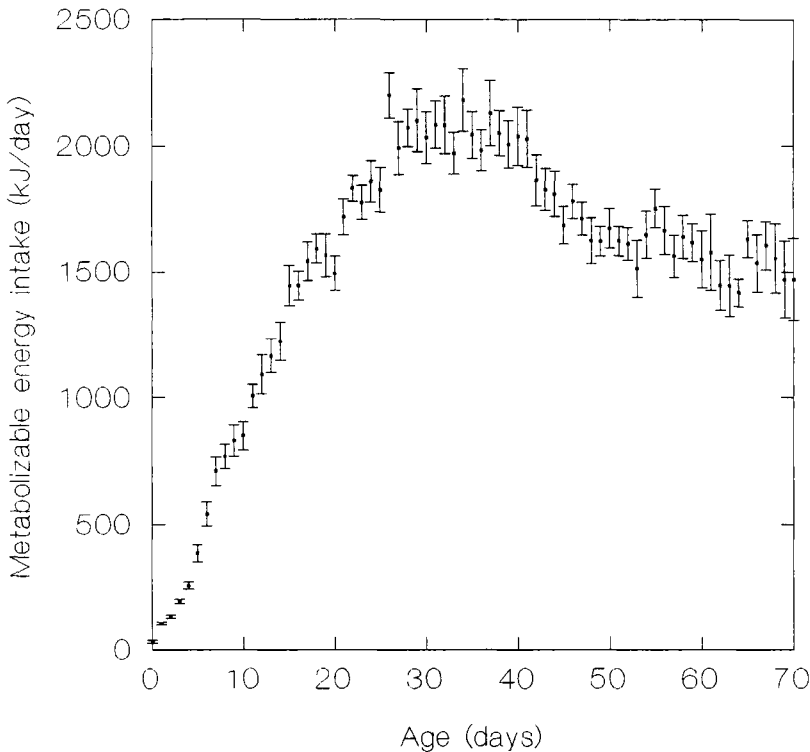


Fig. 2. Daily metabolizable energy intake ($\bar{x} \pm \text{SE}$) of hand-reared Great Blue Heron chicks ($n = 12$) as function of age.

3), and the total gross energy requirement predicted by these budgets reflected the observed gross energy intake of the chicks (Fig. 3). As the chicks grew, their total gross energy requirement and total energy requirement for maintenance increased to a maximum between 30 and 39 days of age and declined thereafter. The total energy requirement for gain was greatest between 10 and 19 days of age for fe-

male chicks and 10 and 29 days 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.

DISCUSSION

Growth of hand-reared Great Blue Heron chicks in our 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 130-4,500 g) indicates that the hand-reared Great Blue Herons in our study grew at a rate to be expected for herons fledging at a mass of 2.3 kg (Table 4, Fig. 4). These comparisons support the use of our method of hand-rearing heron chicks as a suitable model to study the growth and energy requirements of wild Great Blue Heron nestlings.

Energy requirements.—Maintenance energy requirements determined in our study (Table 2) include the requirements for basal metabolism,

TABLE 2. Energy requirements ($\bar{x} \pm \text{SE}$) for maintenance and gain of hand-reared Great Blue Heron chicks ($n = 12$) as a function of age.*

Age interval (days)	E_{MAIN} ($\text{kJ g}^{-0.67} \text{day}^{-1}$)	E_{GAIN} ($\text{kJ g}^{-1} \text{day}^{-1}$)
10-19	$10.79 \pm 0.86^{\text{AB}}$	$7.82 \pm 0.98^{\text{A}}$
20-29	$10.98 \pm 0.83^{\text{A}}$	$7.57 \pm 0.63^{\text{A}}$
30-39	$10.39 \pm 0.29^{\text{AB}}$	$8.90 \pm 0.46^{\text{A}}$
40-49	$9.30 \pm 0.23^{\text{BC}}$	$11.19 \pm 1.59^{\text{B}}$
50-59	$8.47 \pm 0.26^{\text{C}}$	$8.32 \pm 1.12^{\text{A}}$
60-70	$8.21 \pm 0.23^{\text{C}}$	$9.70 \pm 1.42^{\text{A}}$

* Energy requirements determined using method of Hurwitz et al. (1978). Values in given column with superscripts of unlike capital letters differ significantly ($P < 0.05$).

TABLE 3. Calculation of energy budgets (modeled after Ricklefs et al. 1980) of male and female hand-reared Great Blue Heron chicks.*

Age interval (days)	Variables								
	1	2	3	4	5	6	7	8	9
	Male chicks								
10-19	597	73.0	10.79	7.82	781	571	1,352	209	1,561
20-29	1,416	77.4	10.98	7.57	1,418	587	2,005	310	2,315
30-39	2,053	42.7	10.39	8.90	1,722	380	2,102	325	2,427
40-49	2,361	16.4	9.30	11.19	1,693	183	1,876	290	2,166
50-59	2,455	6.2	8.47	8.32	1,581	52	1,633	253	1,886
60-70	2,462	-8.2	8.21	9.70	1,537	-80	1,457	226	1,682
	Female chicks								
10-19	665	73.3	10.79	7.82	840	573	1,413	219	1,632
20-29	1,396	60.1	10.98	7.57	1,405	455	1,860	288	2,148
30-39	1,912	31.6	10.39	8.90	1,642	281	1,923	298	2,221
40-49	2,115	10.4	9.30	11.19	1,572	116	1,688	261	1,950
50-59	2,177	3.7	8.47	8.32	1,488	31	1,518	235	1,753
60-70	2,174	1.1	8.21	9.70	1,414	11	1,425	220	1,646

* Explanation of columns: (1) actual mean body mass (g); (2) actual mean body mass gain (g/day); (3) energy requirement for maintenance ($\text{kJ g}^{-0.67} \text{ day}^{-1}$) from Table 2; (4) energy requirement for gain ($\text{kJ g}^{-1} \text{ day}^{-1}$) from Table 2; (5) total energy requirement for maintenance (kJ/day) is (value 1)^{0.67} × (value 3); (6) total energy requirement for gain (kJ/day) is (value 2) × (value 4); (7) total metabolizable energy requirement (kJ/day) is (value 5) + (value 6); (8) total excreta energy (kJ/day) is $0.134 \times (\text{value } 7)/0.866$; and (9) total gross energy requirement (kJ/day) is (value 7)/0.866.

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 our study were raised under relatively constant temperatures and, presumably, within their thermoneutral zone, as indicated by their behavior (see Materials and Methods). Therefore, the determined maintenance energy requirements would contain a minimal thermoregulatory component.

The decline in E_{MAIN} as the birds grew (Table 2) may represent an accumulation of metabolically inactive tissues, such as adipose, feathers, and skeleton. The low energy requirements of chicks during their first 20 days (Table 3, Fig. 3) should enable parents to spend less time foraging and more time brooding their young. Heron chicks are brooded by their parents for two weeks after hatching (McAloney 1973) and are not fully homeothermic until three weeks of age (Calogeros unpubl. data). During the chicks' first three weeks, female herons mostly feed the chicks (Butler 1991) and at least one parent remains in constant attendance (Pratt 1970). Parents seldom leave the chicks unattended to forage until the young are three weeks old, which coincides with the time of maximum energy requirements of the chicks (Fig. 3).

Energy limitation and reproductive success.—Chicks consumed $2,027 \pm 25 \text{ kJ/day}$ during the time of greatest food consumption (Fig. 2). Therefore, parents must provide 6,100 and 8,100 kJ/day 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. 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.

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 (1,430 kJ/day; Bennett 1993) by the MEC of fish when fed to herons (0.866; Bennett and Hart 1993). Assuming the total metabolizable energy requirements of wild ciconiiforms to be 1.5 times maintenance requirements (Kahl 1964, Siegfried 1969, Kushlan 1977), the metabolizable energy requirement of adult Great Blue Herons is 1,860 kJ/day. Assuming both parents contribute equally to feeding the chicks (Butler 1993), the above provisioning levels (6,100 kJ per brood of three chicks and 8,100 kJ per brood of four chicks) represent a 2.6- and 3.2-fold increase, respectively, in the amount of maintenance energy that the parents must obtain in order to

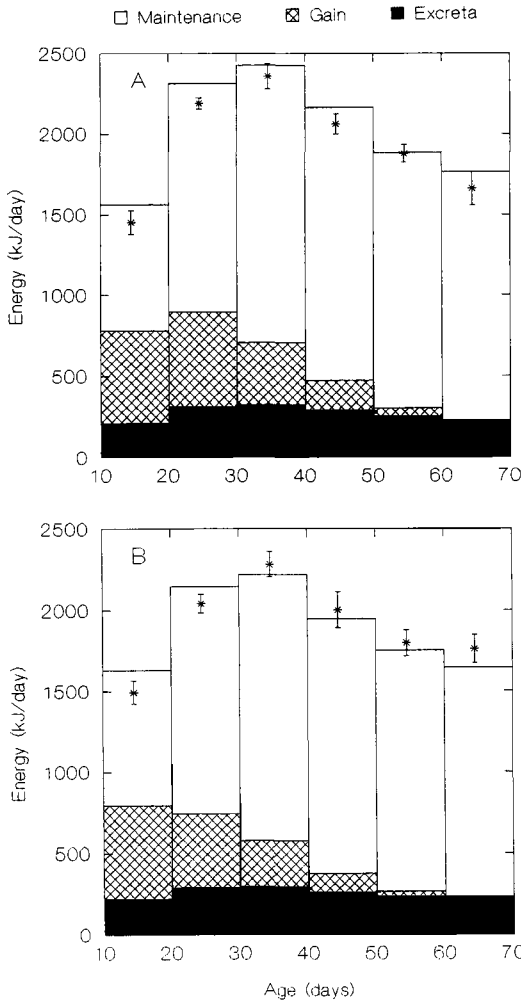


Fig. 3. Energy budgets for (A) male ($n = 8$) and (B) female ($n = 4$) hand-reared Great Blue Heron chicks. Budget calculations presented in Table 3. Asterisks represent observed gross energy intakes ($\bar{x} \pm SE$) of chicks.

meet the energy needs of themselves and their chicks during the time of peak energy consumption of the chicks.

Butler (1993) estimated that the metabolizable energy intakes of adult herons were $4,796 \pm 859$ and $1,797 \pm 170$ kJ/day ($\bar{x} \pm SD$) 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 [Bennett and Hart 1993]). His calculations, based on median dates, indicate that peak food availability to the parents pre-

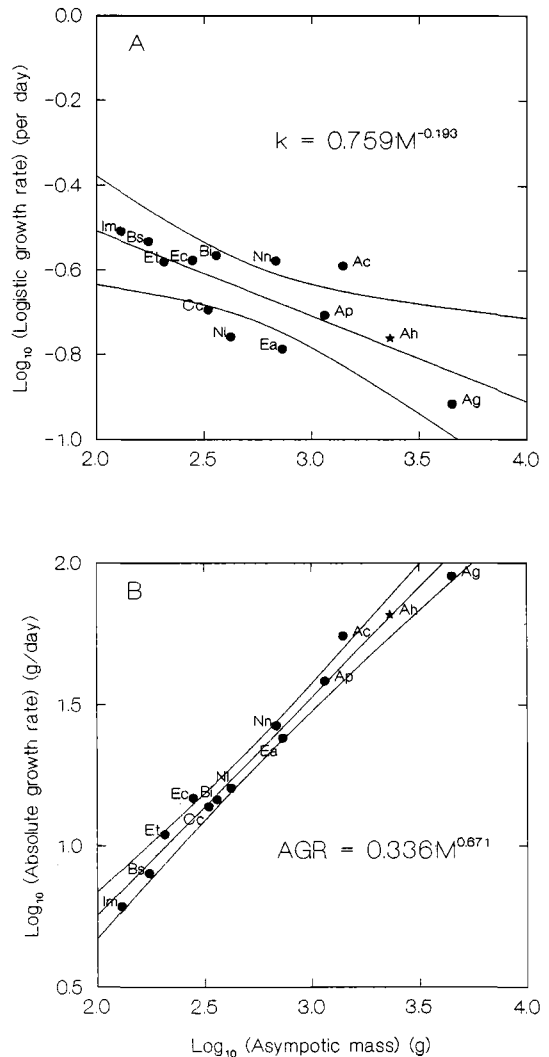


Fig. 4. Relationship between (A) logistic growth rate (k) and (B) absolute growth rate (AGR) with asymptotic body mass (M) for various species of herons (see Table 4 for data and sources). Star symbol represents growth rates of hand-reared Great Blue Heron chicks determined in our study. Key to species: (Ac) *Ardea cinerea*, (Ag) *A. goliath*, (Ap) *A. purpurea*, (Ah) *A. herodias*, (Bi) *Bubulcus ibis*, (Bs) *Butorides striatus*, (Cc) *Cochlearius cochlearius*, (Ea) *Egretta alba*, (Ec) *E. caerulea*, (Et) *E. thula*, (Im) *Ixobrychus minutus*, (Nn) *Nycticorax nycticorax*, and (Ni) *N. leuconotus*.

cedes the peak energy requirements of the chicks.

If adults consume 4,800 kJ/day at the time of peak energy availability (Butler 1993) and have an estimated energy requirement of 1,860 kJ,

TABLE 4. Growth rate and asymptotic mass of various species of herons.

Species	Growth rate		Asymptotic mass (g)	Source
	k^a (per day)	AGR ^b (g/day)		
<i>Ardea cinerea</i>	0.257	55.0	1,402	Owen 1960
<i>A. herodias</i>	0.173	65.6	2,340	Our study
<i>A. goliath</i>	0.121	89.8	4,500	Junor 1972
<i>A. purpurea</i>	0.196	38.2	1,150	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

^a Logistic growth rate.

^b Absolute growth rate.

each parent, on average, could supply the nest with 2,930 kJ/day. If peak energy demands of chicks (2,027 kJ/day) occur 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 1993). 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 traveling 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 1991) and adults often glide to conserve energy (H. de la Cueva and R. W. Butler pers. comm.). Breeding colonies are thought to be located near feeding areas in order to minimize the traveling cost to parents (Gibbs 1991).

Peak mortality of wild Great Blue Heron chicks generally occurs between two and six weeks 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 our study (Figs. 2 and 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 limited largely by the availability of food to the parents.

Sexual dimorphism.—Our study is the first to report sexual dimorphism in body mass for Great Blue Heron chicks. The asymptotic mass of male herons was significantly greater than the asymptotic mass of female herons, and both values are similar to those previously reported for adult herons (Hartman 1961, Simpson 1984). Sexes did not differ in their hatching mass, but by day 30 the male herons were significantly heavier than the female herons (Fig. 1). Quinney (1982) was not able to discern sexual dimorphism in growth of wild herons, probably because his study ended when the birds were 28.5 days old.

There were no significant differences in El_{ME} , nor in the energy requirements between male and female heron chicks in our study. The small sample size (eight male and four female herons), large variability in El_{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.

Our 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 1993) and the chicks' energy requirements (our study) is similar to the observed number of young fledged per successful nest (Forbes et al. 1985, Butler 1989). Peak mortality of wild nestlings (Collazo 1981, Quinney 1982, Pratt and Winkler 1985, David and Berrill 1987, Butler 1989) occurs during the time of peak chick energy requirements as indicated by our study.

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