

TIME OF BREEDING IN RELATION TO FOOD AVAILABILITY OF FEMALE GREAT BLUE HERONS (*ARDEA HERODIAS*)

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ABSTRACT.—I examined the hypotheses that Great Blue Herons (*Ardea herodias*) began breeding in spring shortly after acquiring enough food to make eggs, or so that chicks were in nests when food was most plentiful. Egg laying began about nine days after a female's daily food intake crossed an estimated energy threshold of 1,715 kJ/day. In contrast, the peak in availability of food energy to adults occurred at least 26 days before the peak food demands of their chicks. The estimated food energy intake by adults increased gradually in March and April with increasing duration of low tides and the inshore movement of fishes. Adult food energy intake reached a peak in May when shiner seaperch (*Cymatogaster aggregata*) were most abundant, and diminished through June and July. Received 9 January 1992, accepted 11 April 1993.

LACK (1954) POSTULATED that natural selection favors adults whose nestlings are present when food is most available to the parents. This hypothesis predicts that early and late nesters should fare less well than those nesting on the average date. Several studies have supported Lack's (1954) hypothesis (see review by Perrins and Birkhead 1983), but early clutches in other species are often the most productive (e.g. Cavé 1968, Davies and Lundberg 1985, but see Noordwijk et al. 1981).

Alternatively, Perrins (1965, 1970) proposed that food shortages during egg laying prevent most females from breeding as early as Lack predicted so that young would be in the nest after the parents' food supplies had peaked. Several studies suggest that females breed when food becomes plentiful (Drent and Daan 1980, Daan et al. 1988), but it is not clear whether most young are in nests when food is increasing or decreasing in abundance (see Daan et al. 1988).

Tests of Lack's (1954) and Perrins' (1965, 1970) hypotheses have been hampered by methodological problems. Most studies have used the abundance of food at foraging sites as an index of food availability to the parents rather than measuring food availability itself (see definitions in Daan et al. 1988). Moreover, these hypotheses assume that food is in short supply to the egg-laying female (Perrins 1965, 1970) or adults with nestlings (Lack 1954), although many studies have found that breeding birds are not short of food (see reviews by Martin 1987, Linden and Møller 1989).

A suitable species in which to compare timing of breeding is one in which both food avail-

ability and prey consumption can be measured directly. The Great Blue Heron is a suitable species because: (1) it eats fish whose populations can be sampled with beach-seine nets; and (2) its rate of consumption of fish can be estimated (Simpson 1984, Bayer 1985).

The aim of my paper is to relate the seasonal availability of food energy to heron time of breeding. First, I estimate the relative availability of prey energy to adult herons at three points in time—when they have eggs, small chicks and large chicks. I then examine whether critical food shortages occur by comparing estimates of food energy consumption on the foraging grounds by breeding adults with those of an average-sized brood of heron chicks in the nest. Next, I evaluate the hypotheses that: (1) females begin to lay eggs after a threshold of available energy for egg production has been passed (Perrins 1965, 1970); and (2) chicks are in the nest when food for adults is most plentiful (Lack 1954).

STUDY AREA AND METHODS

Fieldwork.—I studied a colony of 85 to 100 pairs of herons from 21 March to 24 September 1987, and 21 February to 18 August 1988 on Sidney Island (48°40'N, 123°20'W), about 4 km east of the town of Sidney and 23 km ENE of Victoria, British Columbia. Sidney Island is mostly covered in second-growth Douglas fir (*Pseudotsuga menziesii*). The herons nested in red alder (*Alnus rubra*) trees. Littoral drift has created a lagoon (ca. 100 ha) in which most herons fed each day. The first part of the lagoon exposed by falling tides is a salt-marsh community dominated by *Salicornia virginica* and *Distichlis spicata*. Herons used this marsh as a

loafing site. Adjacent to the salt marsh is a 60 ha mudflat that supports sea lettuce (*Ulva lactuca*) and sparse growth of eelgrass (*Zostera marina*). Some herons fed there before and after the tides exposed the most heavily used zone, which was dominated by a dense growth of eelgrass (ca. 30 ha).

Foraging.—Feeding herons were watched through a 15–60× and a 20× spotting scope. I opportunistically chose a feeding heron and recorded over the next 10 min the time of each strike to the nearest second, the type of fish caught (e.g. gunnel, sculpin, etc.), and the estimated total length of the fish as a proportion of the culmen length of the heron (<¼, ¼ to <½, ½ to <¾, ¾ to 1, >1). A female Great Blue Heron in British Columbia has an average culmen length of 123.9 ± SE of 5.1 mm ($n = 29$; Simpson 1984), so these increments represent about 31 mm. I chose 10-min intervals because preliminary observations showed that herons caught a fish about every 2 min.

Relative availability of energy to adult herons.—Relative availability of food energy is the biomass of fish present in the lagoon expressed in units of energy (kJ), multiplied by the duration of low tides (<1.7 m) during each stage of the breeding season. It was estimated from the formula:

$$ME_s = F_s W_s C T_s \quad (1)$$

where ME_s is the amount of available energy in nesting stage S ; F_s is the estimated number of the fish in a fenced area in the lagoon in nesting stage S , W_s is the average mass in grams of fish caught in the fenced area in nesting stage S ; C is a constant multiplier for metabolizable energy content of fish equal to 4.76 kJ/g dry mass (see below), and T_s is the average number of minutes of low-tide foraging in nesting stage S . Each of these terms in the equation is now explained in detail.

Number of fish in lagoon (F).—Some fish species in the lagoon were more easily caught in the beach seine than others. Therefore, a variety of methods was used to estimate the numbers of fish in the lagoon. The numbers of slow-swimming and cryptic species (gunnels [*Pholis ornata* and *P. laeta*], sticklebacks [*Gasterosteus aculeatus*], sculpins [*Leptocottus armatus*] and pipefish [*Signathus griseolineatus*]) were estimated as follows. A polyethylene fence lined with galvanized chickenwire was erected around poles enclosing three sides of a 9 × 9 m portion of eelgrass (*Zostera marina*) bed on an ebbing tide in Sidney lagoon when nests held eggs, small chicks and large chicks in 1988. The fourth side of the fenced area opened toward the beach so that fish would remain in the deeper water inside the fenced area. A 1.5 × 18 m (6-mm stretched mesh) beach seine was pulled along the inside perimeter of the fenced area until it lay alongside the fence. With a person holding each end, the beach seine was quickly hauled through the fenced bed of eelgrass toward the opening. This method was repeated until

most fish had been caught. On each haul, the contents were quickly emptied into separate water-filled buckets. About 20 to 30 min were required to nearly empty the fenced area. Fish caught in seine hauls were identified using Hart's (1973) descriptions. Samples of the catch were weighed with Pesola spring balances, measured (total length) on a fish ruler, and released. These data were used in Leslie and Ricker models (Krebs 1989:162–166) to estimate the number of fish in the fenced area (Butler 1991).

Few shiner seaperch (*Cymatogaster aggregata*) and no tube-snouts (*Aulorhynchus flavidus*) were caught in the fenced area, but both were regularly caught in seine hauls elsewhere in the lagoon. I estimated their numbers by assuming that the proportion of all species caught in 19 seine hauls outside the fenced area each month was the same as in the fenced area prior to its installation. This assumption is discussed later.

Energy estimates in prey (W,C).—All fish caught in the fenced area were measured and samples were weighed to derive length-mass equations for each species (Butler 1991). The mean mass of all fish caught during each nesting stage was converted into units of energy by multiplying by a constant (C) derived as follows. I assumed that: (1) all fish contained 71% water (Holmes and Donaldson 1969); (2) the assimilation efficiency of herons was 77% (Castro et al. 1989); and (3) each gram dry mass of fish contained 21.3 kJ (Cummins and Wuycheck 1971). Therefore, the constant:

$$C = (1 - 0.71 \text{ g dry mass})(0.77) \\ (21.3 \text{ kJ/g dry mass}) = 4.76 \text{ kJ/g dry mass.}$$

Nesting stages (S).—Heron nests on Sidney Island were built about 20 m above the ground in the tree canopy; therefore, they could not be checked directly. I estimated each nesting stage from the median date that the first-hatched egg shell was found below each nest. The respective median hatching dates in 1987 and 1988 were 14 and 19 May. The chick stage was divided in one-half so that nests were defined as containing small chicks from 14 May to 8 June (ca. first three weeks), and large chicks from 9 June to 1 July (ca. fourth through sixth week). Incubation requires about four weeks (Vermeer 1969, Brandman 1976). Therefore, the incubation stage was back-dated 28 days from the median hatching date to include the period 15 April to 13 May. Egg laying was estimated to occur from 1–14 April.

Duration of low tides (T).—Tides are measured from the lowest, low tide (0.0 m) and the tidal amplitude in Sidney lagoon is about 3.0 m. Herons could wade in the eelgrass foraging areas when tides were less than about 1.7 m. I assumed that all herons on beaches fed through the entire low-tide period because none were engaged in other activities, and trips to nests to feed chicks were brief at this time (I. Moul pers. comm.). The number of minutes of low tide available to foraging herons each day of the breeding season

was generated by computer using tidal data from the Tidal Office of the Institute of Ocean Sciences.

Estimated energy consumption by adult herons.—The length of each fish caught by herons was estimated as a proportion of the heron's culmen length. The most significant bias in this method is the observer's ability to estimate the length of the prey (Bayer 1985). Observer precision was tested by showing a range of sizes of the four major prey species held between the mandibles of a dead heron to observers using spotting scopes 65 to 100 m away. Significant differences did not occur between observers ($X^2 = 1.86$, $df = 6$, $P = 0.8$). Two observers correctly identified all fish and underestimated the lengths of some fish sizes by one size class. Therefore, I adjusted fish-length estimates by one size class to reduce observer bias and then converted each fish into energy units following the methods outlined above.

Energy threshold for laying.—Ciconiiformes require about 30% energy above maintenance costs to fuel their activities (Kushlan 1977). The estimated maintenance cost from Kendeigh's (1970) equations for a caged 2,100-g heron is 1,200 kJ, and her activity costs were an additional estimated 360 kJ (30% of 1,200 kJ) for a total daily energy need of 1,560 kJ.

Twenty-seven heron eggs collected in British Columbia near the beginning of the laying period contained a mean of 4.77 g of fat and 3.03 g of carbohydrate plus protein (P. Whitehead unpubl. data). Each gram of fat contains about 39 kJ of energy while a gram of carbohydrate and protein holds about 18 kJ (Blem 1990). Therefore, there are about 240 kJ in an average heron egg. The efficiency of converting metabolized energy into eggs is estimated to be about 70% (King 1973), so an average female musters about 312 kJ per egg. Since herons lay eggs in about two-day intervals (Vermeer 1969), a female requires about one-half the 312 kJ per day (Murton and Westwood 1977) or 155 kJ. She also requires energy for oogenesis for a few days prior to egg formation (Murton and Westwood 1977). The mean clutch size in British Columbia colonies is four eggs (Butler 1989). Therefore, a female heron in British Columbia must exceed a threshold of about 1,715 kJ (1,560 kJ/days for maintenance + 155 kJ/days for each egg) for at least 10 days (Murton and Westwood 1977) to complete her four-egg clutch where one egg is laid every two days. Energy requirements for egg laying will vary elsewhere in the heron's range because clutch size generally increases with latitude (Butler 1992).

Energy consumption by egg-laying females.—I assumed that herons caught most of their food in Sidney lagoon. Most herons foraged in the lagoon during the day when tides were low, and eggs were laid in April (94.1%, $n = 271$). The gender of many herons can be determined by measuring culmen length (Butler et al. 1990). A sample of 18 herons in the lagoon when eggs were laid indicated that all were females. Herons stopped feeding in the lagoon when tides flooded the

beaches in the afternoon and soon after they returned to their nests for the night. Later, when nests held chicks, most herons ($n = 77.7\%$, $n = 1,001$) continued to forage in the lagoon during low tides and returned briefly to nests to feed chicks. Few feedings occurred at night when tides were generally high (I. Moul pers. comm.). Therefore, I used the duration of the low tide each day as a minimum estimate of the amount of available foraging time to herons. Available energy to females before and while they laid eggs was estimated by multiplying the mean daily energy ingestion rate during the egg-laying stage (1–14 April) by the number of minutes that low (<1.7 m) tides uncovered the eelgrass bed each day from 1 February to 14 May.

Food demands of heron chicks.—Twelve chicks were reared from the egg in captivity and fed fish *ad libitum* (Bennett 1993). They were kept indoors in an incubator for about three weeks after hatching to correspond with the period when they would have been brooded in nests by the parents. They were moved to outdoor aviaries at about three weeks of age. The mean mass of fish eaten by chicks each day was converted into units of energy (kJ) using the same methodology used to estimate food energy consumption by wild adults. The mean daily energy consumption of the chicks was used to estimate the age when the maximum food demand occurred. Growth curves of captive-reared (this study) and wild (Quinney 1982) chicks do not differ significantly, and captive-reared herons in this study grew at the expected rate for their body mass when compared to growth rates of 13 species of wild herons (Bennett 1993).

RESULTS

Relative availability of food energy in lagoon.—Herons caught tube-snouts, sticklebacks, shiner seaperch, pipefish, sculpins, and gunnels. The average length, mass and estimated energy contained by these fish through the breeding season is given in Table 1.

Numbers of prey individuals in the lagoon were greatest by far when herons had small chicks in nests ($3,297 \pm SE$ of 6) compared to when nests held eggs (360 ± 48) and large chicks (403 ± 5). Low tides exposed the eelgrass habitat for the longest period (216 min per average day) when large chicks (9 June–1 July) were in nests compared to 151, 176 and 208 min per average day when eggs were being laid, were incubated, and when small chicks were in nests, respectively. However, the relative estimated availability of food energy was greatest when small chicks were present (Fig. 1).

Seasonal energy consumption by adults, chicks,

TABLE 1. Average lengths of fish caught in beach seines, their estimated mass from length-mass regression equations and their estimated metabolized energy (calculated from masses) available to herons from major prey species each spring and summer month of 1987-1988 in lagoon at Sidney.

	<i>n</i>	Total length (mm; $\bar{x} \pm SD$)	Mass (g; $\bar{x} \pm SE$)	Metabolized energy (kJ; $\bar{x} \pm SE$)
<i>Pholis ornata</i>				
April	18	87.0 \pm 28.1	1.8 \pm 0.2	8.6 \pm 0.2
May	141	80.8 \pm 19.7	1.3 \pm 0.1	6.2 \pm 0.1
June	92	99.0 \pm 17.2	2.6 \pm 0.1	12.4 \pm 0.1
July	73	94.3 \pm 16.5	2.3 \pm 0.1	11.0 \pm 0.1
<i>Gasterosteus aculeatus</i>				
April	27	60.8 \pm 6.1	1.8 \pm 0.8	8.6 \pm 1.0
May	98	67.2 \pm 5.5	2.6 \pm 0.4	12.4 \pm 0.5
June	42	70.4 \pm 4.4	3.0 \pm 0.7	14.3 \pm 0.9
July	12	73.8 \pm 4.8	3.5 \pm 1.2	16.7 \pm 1.5
<i>Leptocottus armatus</i>				
April	21	64.1 \pm 15.2	2.9 \pm 3.2	13.8 \pm 4.1
May	47	66.4 \pm 24.5	3.1 \pm 1.7	14.8 \pm 2.2
June	66	90.9 \pm 38.5	6.4 \pm 1.5	30.5 \pm 1.9
July	58	95.8 \pm 22.9	7.6 \pm 1.5	36.2 \pm 1.9
<i>Cymatogaster aggregata</i>				
May	15	110.0 \pm 34.2	24.9 \pm 6.7	118.5 \pm 8.6
June	119	104.1 \pm 12.1	21.1 \pm 2.4	100.4 \pm 3.1
July	50	52.1 \pm 5.3	12.0 \pm 3.7	57.1 \pm 4.7
<i>Sygnathus griseolineatus</i>				
April	7	138.0 \pm 58.0	3.9 \pm 0.7	18.6 \pm 0.9
May	118	156.7 \pm 48.2	4.4 \pm 0.2	20.9 \pm 0.2
June	31	173.1 \pm 39.2	4.8 \pm 0.4	22.9 \pm 0.5
July ^a	31	173.1 \pm 39.2	4.8 \pm 0.4	22.9 \pm 0.5 ^a
<i>Aulorhynchus flavidus</i>				
April	5	158.8 \pm 47.3	35.3 \pm 7.56	168.0 \pm 9.7

^a No pipefish caught in seines in July, so I assumed those caught by herons were same size as in June.

and egg-laying females.—Adult herons ingested nearly four times more food energy per day when small chicks were in their nests (Table 2) than when they were laying ($P < 0.001$) or incubating ($P < 0.001$) eggs, and nearly three times as much as when raising large chicks ($P < 0.05$, Kruskal-Wallis ANOVA and multiple-comparison test; Zar 1984:200). The surge in energy consumption resulted from the large number of shiner seaperch in the diet (Table 3).

The greatest food demands by 12 captive-reared chicks plateaued between 26 and 41 days of age ($\bar{x} = 2,027$ kJ·chick⁻¹·day⁻¹; Bennett 1993). The median hatching dates in 1987 and 1988 at Sidney were 14 and 19 May, respectively. Therefore, the estimated peak food demands would have begun 26 days later on about 9 to

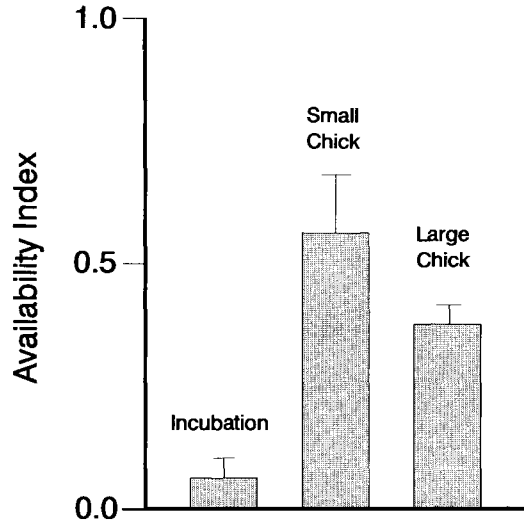


Fig. 1. Index of food availability during breeding season of Great Blue Heron. Percent availability estimated from the product of numbers of minutes when low tides (<1.7 m) exposed foraging habitat and size of fish population converted into units of energy. Whiskers are standard errors.

14 June when large chicks were in nests and when adult ingestion rates were relatively low (Table 2).

One adult forages while its mate tends to the nest in the first two to three weeks after the eggs hatch. Most heron nests on Sidney Island held two or three chicks at the end of the small chick stage. The average adult heron caught about 4,200 kJ per day (Table 2) and expended about 1,500 kJ per day, leaving an estimated 2,700 kJ to be fed to chicks. If the food was equally shared between two brood mates, then one parent could supply each chick an average of 1,350 kJ per day. Each chick in a brood of three would receive about 900 kJ per day. The mean daily ration of 12 chicks in captivity reached 900 kJ at about 12 days of age and 1,350 kJ at about 17 days of age (Bennett 1993). Therefore, one parent could supply the food energy needs of two or three chicks for the first 12 to 17 days. However, food is not shared equally by small chicks (Mock 1987), so one parent could probably provide for the needs of the brood since food demands might be spread over a few more days than indicated by my estimate. Moul (1990) found that nest attendance by one parent fell from 80% of the time when the median age of chicks was 12 days old to 20% when they were 22 days old in the Sidney colony in 1988.

TABLE 2. Estimated metabolized energy intake (kJ) per average day by an adult heron averaged over four periods of breeding season on Sidney Island in 1987-1988 (*n* is number of herons watched).

	Egg laying (<i>n</i> = 27)	Incubation (<i>n</i> = 155)	Small chick (<i>n</i> = 48)	Large chick (<i>n</i> = 109)
Metabolized energy intake rate (kJ/min)	7.7 ± 3.7	6.8 ± 1.1	20.5 ± 3.7	7.4 ± 0.7
Minutes available to forage per day	151	176	208	216
Estimated intake per day (kJ/day)	1,163 ± 555	1,197 ± 194	4,264 ± 764	1,598 ± 151

Egg laying began when the adults' estimated daily energy ingestion exceeded the females' energy threshold for egg laying for seven days in 1987 and nine days in 1988 (Fig. 2). Moreover, available energy fell below the egg-laying threshold for 10 continuous days in late February through early March compared to only one to two days in early May (Fig. 2).

In summary, (1) demands of the chicks occurred several weeks after the peak in availability to their parents, and (2) female herons laid their eggs soon after the estimated egg-laying threshold had been exceeded. I conclude that my findings best support the energy-threshold hypothesis (Perrins 1965, 1970).

DISCUSSION

Validity of assumptions.—In this analysis I assumed that: (1) the relative abundance of fish in the fenced area represented the fish population elsewhere in the lagoon; (2) the proportion of tube-snouts and shiner seaperch caught in seine hauls in the lagoon closely reflected their abundance relative to other species in the lagoon; (3) each fish contained 71% water and 21.3 kJ per gram dry mass of which 77% was assimilated by herons; (4) egg shells were found below nests on the day they hatched; and (5) female herons required 1,560 kJ per day to maintain themselves and an extra 155 kJ each day to produce an egg.

Departures from all of these assumptions contribute additional error to the estimates of energy availability and consumption. However, these errors do not alter my conclusions because the relative abundance of prey populations was more than eightfold greater when small chicks were in nests than when large chicks were present. Moreover, my estimates of the numbers of shiner seaperch in the lagoon might be lower than the actual numbers present because this schooling species could quickly swim away from the beach seine.

The additional errors from estimating water and energy content of fish, assimilation rates, and maintenance energy requirements of herons also are probably low (see Kahl 1964, Dunn 1975, Kushlan 1977, 1978, Castro et al. 1989). For example, a sample of 12 prey fishes in my study contained 71 to 73% water, and three shiner seaperch contained about 3 kJ less energy than my estimate (118 kJ) using values from the literature.

The estimated maintenance energy of 1,200 kJ derived from Kendeigh's (1970) equations was nearly identical to the 1,242 kJ estimate from inactive herons held in outdoor cages at the University of British Columbia in April (Bennett 1993). I have less confidence with my estimates of energy consumption early and late in the nesting season. My energy-threshold estimate for egg laying using published values (1,715 kJ) was greater than my field estimate

TABLE 3. Numbers (with percent in parentheses) of each of main prey species eaten by Great Blue Herons during 1,320 min of observation in 1987-1988 breeding seasons on Sidney Island.

Species	Courtship	Egg	Small chick	Large chick	Total
Gunnel	20 (41.7)	188 (40.9)	56 (34.6)	175 (65.3)	439 (46.8)
Stickleback	0 (0.0)	42 (9.1)	10 (6.2)	8 (3.0)	60 (6.4)
Sculpin	2 (4.2)	78 (17.0)	9 (5.5)	53 (19.8)	142 (15.1)
Seaperch	0 (0.0)	20 (4.3)	68 (42.0)	11 (4.1)	99 (10.6)
Pipefish	0 (0.0)	4 (0.9)	9 (5.5)	1 (0.4)	14 (1.5)
Tube-snout	11 (22.9)	1 (0.2)	0 (0.0)	1 (0.4)	13 (1.4)
Unknown	15 (31.2)	127 (27.6)	10 (6.2)	19 (7.0)	171 (18.2)
Total	48	460	162	268	938

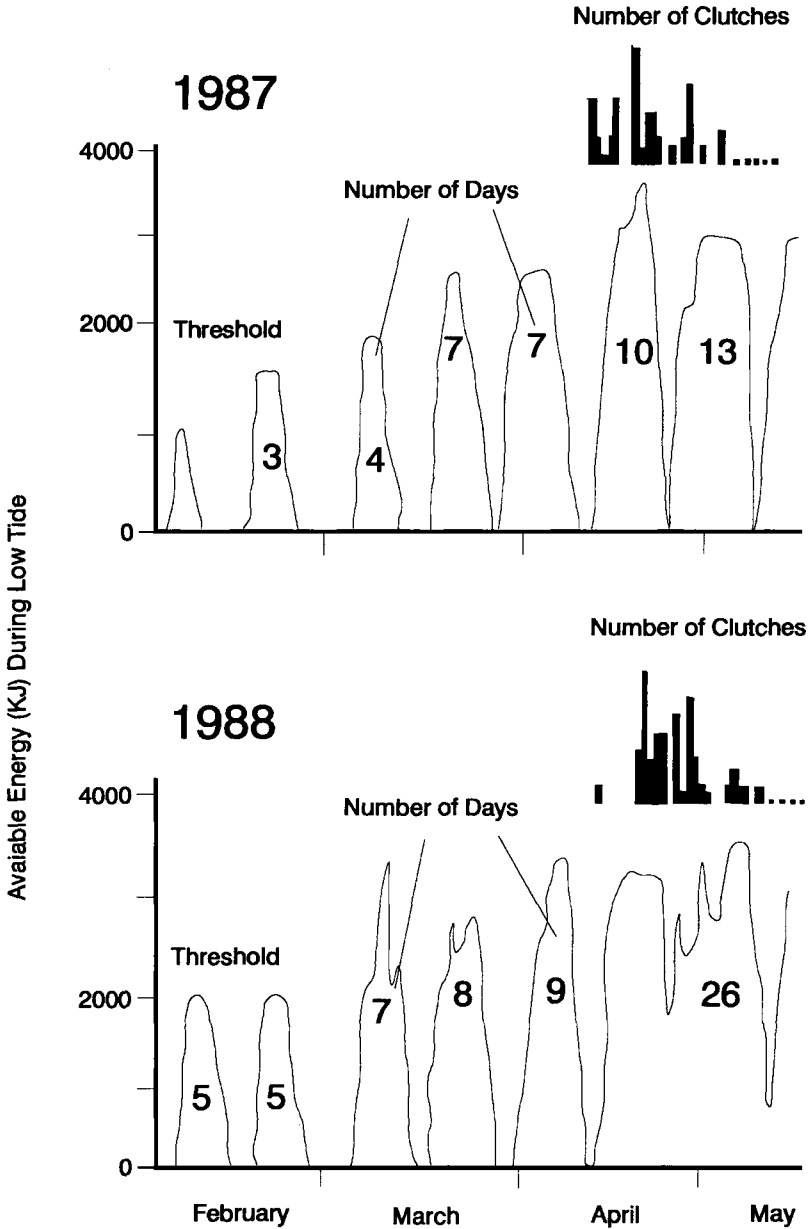


Fig. 2. Numbers of days that available energy exceeded an estimated energy threshold for egg laying, and estimated dates when clutches were laid in 1987 and 1988.

(i.e. 1,163 kJ) of energy ingestion by laying females, but the error around my estimate was great (Table 2). Moreover, I did not account for the small amount of food caught outside the lagoon during high tides. Nevertheless, my conclusion is robust because a large change in the position of the threshold is required to make

a small change to the number of days when food availability exceeds the threshold in Figure 2.

The general pattern of foraging activity by the Sidney herons was dictated largely by the position of the tides. The lowest tides occurred during the day when most herons foraged in

Sidney lagoon. As the tide flooded the beach mostly in the afternoon, herons gradually flew to nearby trees to digest their meals or to the colony to feed the chicks. Small numbers departed the island through the afternoon and evening to forage or rest along nearby beaches until the next morning when they returned to the colony site. I assumed that most food eaten by herons and fed to their chicks was caught in Sidney lagoon because: (1) most herons foraged there during the most productive foraging time when tides were lowest; (2) the best foraging habitats were eelgrass beds, which were covered by water each evening; and (3) chicks were rarely fed at night when herons foraged off the island (I. Moul pers. comm.). Nonetheless, herons that met some of their energy needs at night could devote more time during the day to foraging for their chicks. However, adult herons did not have the option of foraging both day and night until chicks were two to three weeks old. Therefore, my values of energy ingestion are probably minimum estimates.

Time of breeding.—My results are best explained by Perrins' (1965, 1970) hypothesis that: (1) energy availability determines when females will lay eggs; and (2) chicks are in the nest after food availability to their parents has peaked. However, most females laid eggs several days after the estimated threshold had been crossed (Fig. 2). Some of this variability probably arose from females being in different body condition (see Drent and Daan 1980, Perrins and Birkhead 1983). Thus, the Great Blue Herons on Sidney Island during my two-year study faced a difficult optimization problem: once females crossed the threshold for egg laying, an insufficient time remained for the chicks to match their food demands with the peak in the food supply. Only one parent is available to forage when small chicks are in nests and food is most available because small chicks require near constant brooding. Both parents are available to forage for large chicks after food availability peaks.

However, it is possible that herons coincidentally might match the peak demands of their growing chicks to the time of year when prey is most abundant in other years and at other locations. The time of peak food abundance varies between years and locations (Kelsall and Simpson 1980, Bayer 1981). However, the precise timing of peak food availability at any location is likely to be too variable to predict by

a female heron preparing to lay eggs one to two months earlier in April, as posited by Lack (1954).

It is unlikely that photoperiod or air temperature are significant influences (see references in Orell and Ojanen 1983) on when herons breed because laying dates are not synchronized between nearby colony sites. For example, in two years of this study, three colonies in the Fraser River delta (30–40 km to the north) and a colony in Victoria (25 km to the southeast) hatched eggs two to three weeks earlier than Sidney. Moreover, a colony near Crofton (35 km to the west) hatched eggs in the same week as Sidney. I hypothesize that the asynchrony in laying dates between colonies results from differences in inshore movements of local fish populations.

The daily duration of low tides determines how much food herons acquire throughout the year (Fig. 2). Female herons might store energy on winter days when tides were very low (Butler 1991, Bennett 1993) to safeguard against predictable periods of food scarcity. Here, I propose that, as periods of food scarcity become less frequent in spring, female herons devote less foraging time to maintaining their energy balance and more time to the breeding effort.

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