Diet and behaviour of young American Coots

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Introduction

Only fragmentary information exists on the diets of young American Coots *Fulica americana* (Jones 1940; Sooter 1941; Fredrickson 1977; Fitzner *et al.* 1980). Neither temporal changes in diet nor the various foraging techniques of young have been studied.

Qualitative and quantitative studies on the behavioural ecology of adult American Coots exist (Gullion 1952, 1953, 1954; Fredrickson 1970; Ryan and Dinsmore 1979, 1980), but quantitative measurements of the activities of the young are lacking. The allocation of time and energy for functions such as feeding and growth would indicate how young Coots cope with the complexities of their environment, and the assessment of these functions would provide an additional means of understanding the ecological niche of the species (*sensu* Pianka 1978). Time-activity budgets not only provide an evaluation of various biological costs to the individual, but also provide a means of measuring the degree of interaction between young and parent. Adult birds are known to invest considerable time and energy on the welfare of their young (Walsberg 1983).

The questions asked in this study were: (1) does the composition of the diet of young Coots change with time; (2) do the patterns of feeding behaviour change with time of day and growth of young; (3) what interactions between young and adult Coots occur during feeding, and do they change with the growth of young; (4) do the patterns of non-foraging activities change with time of day and growth of the young, and (5) what are the biological costs expended by young, and by adult Coots on behalf of the young.

Study Area

Young Coots were observed and collected from 23 wetlands in the aspen parkland of Saskatchewan (Bird 1961), 45–75 km NE of Saskatoon. This area of undifferentiated glacial till is characterised by moderate to hilly terrain with wetlands in many of the depressions. Approximately 70% of the land is cultivated. Cereal grains and canola *Brassica napus* are the major crops. The study ponds averaged 0.75–1.5 m in depth and 0.5–40 ha in area. These ponds are eutrophic and alkaline, with pH between 7.9–9.2 (Driver and Peden 1977). The communities of these wetlands were complex and included 12–30 species of Chironomidae (Driver 1977), 4–8 species of Trichoptera (Smith 1975), and 10-25 species of Hemiptera (Brooks and Kelton 1967; Driver *et al.* 1974; Stelfox 1977; Driver 1981). Zooplankton, mainly *Daphnia magna, D. pulex, D. middendorffiana* (Driver, unpublished) and *Diaptomus arcticus* and *D. forbesi* (Sawchyn 1966; Hammer and Sawchyn 1969), occurred chiefly at the mergent-submergent vegetation interfaces. The dominant emergent vegetation included whitetop *Scolochloa festucacea*, cattail *Typha latifolia*, bulrushes *Scripus acutus* and *S. americanus*, and sedges *Carex* spp., while submergent vegetation comprised primarily pondweeds *Potamogeton pectinatus* and *P. richardsonii* and water milfoil *Myriophyllum exalbescens* (Millar 1973, 1976) occurring in patchy to dense stands.

Materials and Methods

From 1 June–31 August, 1977–1979, young Coots were collected by shot-gun. Young were divided into three size classes relative to adult size: <1/3 (Class A), 1/3–2/3 (Class B) and >2/3 (Class C).

Intact young Coots were weighed in the field to the nearest 0.1 g, and were frozen upon return to the laboratory. Body measurements (head length, width and height; leg and leg component lengths; bill length, width and height; and total body length) as well as colour and other plumage characteristics were recorded from thawed birds. On the basis of plumage characters (Gullion 1954) and body measurements, Class A Coots were 1–29 days old; Class B were 30–59 days old and Class C were 60 or more days old.

Only young that were observed feeding for 10–15 minutes were collected to ensure the recovery of ingested food items. Im-

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mediately after collection, the upper digestive tract (oesophagus, proventriculus, and gizzard) was removed and placed in 75% ethanol. The digestive tract contents were sorted, dried at 80°C for 24 hrs and weighed. Gastropod weights included the shell, but Trichoptera larval cases constructed of sand and shell fragments were excluded from the analysis because they were considered of limited nutritional value. The data were reduced to an aggregate mean percentage (Swanson *et al.* 1974) of dry weight and percentage occurrence.

Invertebrate communities were sampled immediately after young were collected and at times immediately following the recording of time-activity bouts. Replicate sweeps (Sudgen 1973; Swanson *et al.* 1974) were taken at each of eight wetlands where time-activity bouts were recorded. An additional series of replicate sweep samples were taken at the 15 ponds where young were collected.

Coot family units (young with or without an adult), were observed, with a 20x spotting scope or 7 x 50 binoculars, for half hour intervals between 0500 and 2000 hours. Adult behavioural activities were recorded separately, and sexes pooled. The activities of the young were recorded according to size class. All activities were recorded to the nearest minute. Movements of broods were recorded on maps in order to determine the brood association with wetland margins. Feeding activity was recorded for six categories: fly catching, pecking, diving, neck extended, tipping and begging. Descriptions of these behaviours are found in Goodman and Fisher (1962), Sudgen (1973) and Gullion (1952, 1954). Other activities included swimming (without foraging), preening (all plumage maintenance), and loafing. The seven aggressive displays described by Gullion (1952) were pooled as one for this study.

Time-activity budgets were computed from direct observations. The number of bird-minutes spent out-of-sight (shielded by the vegetation) was not used in determining percent activity.

The time young Coots spent in a day on various activities was converted to time energy budgets by increasing the maintenance energy (EM) calculated at an ambient temperature of 18°C (Kendeigh *et al.* 1977) by the relative costs of various activities. The costs were: 3.0x for aggression; 2.5x for feeding; 2.0x for locomotion; 2.0x for night time activity; 1.5x for preening; 1.5x for resting and sleeping (King 1974; Dwyer 1975). All values, except night time activity (no observations), were reduced by 0.667 (Table 4). Night time energy expenditure was multiplied by 0.333. These results were then compared with the calculation of daily energy budgets (DEB) for young growing birds (Kendeigh *et al.* 1977).

Energy costs of adults were calculated from maintenance metabolism equations at an ambient temperature of 18°C (20°C for Iowa), and mean adult weight of 550 g (Tordoff and Mengel 1956; Fredrickson 1969; Alisauskas and Ankney 1985). Activity data, from this study and from Ryan and Dinsmore (1979), were used to estimate the components of time energy budgets (TEB).

Results

Diet

Invertebrates recovered from the upper digestive tract excluding the gizzard were easily identified. In 65 young Coots (29 Class A, 26 Class B, 10 Class C) with food in the upper digestive tract, the mean dry weight of food was 25.2 mg (range 10–232 mg). The average dry weight of animal food items was 8.8 mg (range 0.3–17.8 mg). As the Coots grew, they ate progressively less animal foods (Table 1, x^2=26.6, df=2, P<0.001).

In Class A young, invertebrates represented 84% of the diet, of which insects comprised 91%. Class A Coots concentrated on animal food, and showed no preference for specific plant items. The major aquatic macrophytes, *Myriophyllum* sp., *Carex* spp., *Potamotegon* sp., were eaten in equal proportions along with lesser amounts of a floating filamentous alga, *Cladophora* sp. Half of the invertebrates eaten by Class A Coots were taken at lower proportions than their occurrence at feeding sites (Table 2, G=25.60, df=7, P<0.001). Several food items eaten including insect eggs, cocoons of the leech *Erpodbella* sp., and moth larvae *Bellura* sp., are closely attached to aquatic vegetation, and rarely collected during sweep sampling.

There was no difference in the selection of diet items by Class B and C Coots (G= 3.89, df=7, P>0.20). They preferred trichopteran larvae *Limnephilus* sp., adult and larval dysticid beetles and pond snails

Table 1. Food items recorded in digestive tracts of young American Coots in Saskatchewan.

	Dry weight (%)			Occurrence (%)		
Age class	A	B	C	A	B	C
Number analysed	29	26	10	29	26	10
Plant						
Cladophora sp.	3	7	1	3	8	10
Chara sp.	–	–	2	–	–	10
Potamogeton spp.	4	19	20	14	19	30
Carex spp. nutlets	4	1	–	7	4	–
Scirpus spp. nutlets	<1	5	<1	3	12	10
Lemna spp.	<1	23	40	3	35	40
Myriophyllum sp.	5	5	16	14	19	30
Unidentified seeds	–	1	–	–	4	–
Plant food subtotal	16	61	79	34	73	100
Animal						
Hirudinea	1	<1	–	13	4	–
Crustacea (Eubranchiopoda)	–	1	–	–	4	–
Insect eggs	8	–	–	7	–	–
Odonata (Zygoptera)	6	–	–	7	–	–
Hemiptera	2	5	<1	10	12	10
Trichoptera larvae	18	9	2	28	15	10
Lepidoptera larvae	<1	8	<1	3	8	10
Coleoptera	31	11	8	48	23	20
Diptera larvae	9	<1	1	21	8	20
Gastropoda (Physidae)	9	6	10	17	15	20
Animal food subtotal	84	39	21	90	65	30

Table 2. Comparison of invertebrate items observed in the diet of young American Coots and sampled in the wetlands in which the young had fed.

	Percent Occurrence			
Food Items	Class A		Class B & C	
	Coot (29)	Environment (24)	Coot (36)	Environment (48)
Annelida	9.5	3.0	3.5	<0.5
Crustacea	<0.5	15.0	3.5	19.0
Odonata	4.8	12.0	<0.5	9.0
Hemiptera	7.1	20.0	14.0	30.0
Trichoptera	19.0	6.0	17.0	2.0
Coleoptera	33.0	20.0	27.0	22.0
Diptera	14.2	16.0	14.0	16.0
Gastropoda	11.9	7.0	20.5	1.5

Physa sp. When Class B and C young were combined they exhibited a selection pattern similar to Class A young (G=38.8, df=7, P<0.001). There was no difference in the use of invertebrates eaten by either Class A or the older classes (G=2.93, df=7, NS), nor in the temporal distribution of the invertebrates collected from the various wetlands (G=10.78, fd=7, P>0.10). The proportion of plant material eaten increased 45% from Class A to Class B, and increased by 18% from Class B to Class C. The selection of plant foods narrowed to two genera, *Lemna* and *Potamogeton*. The former is usually at maximum biomass between mid-July and early August, the period when most Class B and C young were collected.

Grit

Of 75 young Coots examined for grit content, only 25% of Class A young, and specifically the youngest of this class, did not contain grit. Young without ingested grit often contained egg shell fragments in the digestive tract. Class A young averaged 0.35±0.09 (standard error) g (n=44, range 0.01–10.3 g), Class B contained 2.73±0.39 g, (n=21, range 0.65–5.73 g), and Class C birds the grit content averaged 4.7±0.94 g, (n=10, range 2.5–8.6 g). The grit content was significantly different between each of the three age classes (t-tests, P<0.001) and increased with age.

Foraging behaviour

Class A young spent 30-50% of their foraging time begging food from adult birds (Table 3). The begging activity diminished with age (x^2=40.24, df=2, P<0.001), and was rarely observed in Class C Coots. Along with begging, two other feeding techniques, pecking and extended head and neck, were employed by Class A young to gather food. They pecked at food items near, or on, the water surface, and pecked at bright objects, such as insect parts or vegetation, on dried mats of roundstem *Scripus acutus* or three-square bulrush *Scripus americanus*. The extended head and neck technique was used to capture items just below the water surface or from overhanging vegetation. Ninety-five percent of the foraging by Class A young was concentrated in a 15 m zone along the margin of wetlands >6 ha in size. In shallow wetlands with widely dispersed vegetation, or in small shallow wetlands of <0.5 ha, the entire surface was used.

In Class B and C Coots, diving became the most frequent method of feeding. Class B young used a greater variety of feeding techniques than the other age classes (Class A $\bar{x}$=4.67, Class B $\bar{x}$=6.0, Class C $\bar{x}$=2.67), but these techniques apparently did not increase the resources available to them. They did not use other prey (Table 1) nor selected other sizes of prey from the limnetic zone. Class C Coots used primarily two feeding techniques, pecking and diving (Table 3).

Unlike young waterfowl which actively feed early in the morning and again late in the day, young Coots fed throughout the day with only slight variability in feeding intensity (x^2=2.07, df=2, NS). Class C birds fed less between 0500–1000 hours than

Table 3. Percent feeding and other behaviour activity of young (Class A to C) and attendant adult American Coots in central Saskatchewan.

Time	Age Class	Feeding Activity (%) F*	P	D	HN	T	B	Sub-Total	Other Activities (%) S	L	PR	R	AG	A	Sub-Total	Number of Individuals	(minutes)
Period I 0500–1000 hrs	Adult	–	12.9	16.0	2.0	–	–	(30.9)	24.1	15.1	13.1	13.1	3.5	–	(68.9)	15	(60)
	A	0.8	13.6	0.4	1.5	–	17.0	(33.3)	36.4	14.5	4.0	11.4	0.3	0.1	(66.7)	69	(1500)
	Adult	–	44.9	7.0	–	–	–	(51.9)	–	32.7	1.9	4.0	8.8	0.7	(48.1)	40	(430)
	B	0.1	66.4	3.7	0.3	0.5	3.5	(74.5)	–	18.5	4.2	2.5	0.1	0.1	(25.4)	111	(2815)
	Adult	–	5.0	–	–	–	–	(5.0)	–	90.0	–	–	5.0	–	(95.0)	12	(20)
	C	–	5.4	5.4	–	–	–	(11.0)	–	73.0	–	16.0	–	–	(89.0)	18	(177)
Period II 1000–1600 hrs	Adult	–	18.1	14.8	1.1	1.4	–	(35.4)	0.5	34.5	16.2	9.6	3.5	0.2	(64.5)	22	(426)
	A	0.3	17.2	0.4	6.5	t	15.6	(40.0)	6.5	32.3	6.4	14.7	0.1	–	(60.0)	65	(1257)
	Adult	–	31.7	9.9	0.3	0.1	–	(42.0)	–	45.7	3.8	3.4	4.9	0.2	(58.0)	88	(841)
	B	0.6	54.7	5.9	0.1	0.7	1.7	(63.7)	–	28.3	2.2	5.6	–	–	(36.1)	250	(5836)
	Adult	–	17.6	6.3	1.3	–	–	(25.2)	–	62.1	4.1	7.7	0.9	–	(74.8)	24	(222)
	C	–	27.1	5.5	–	–	0.2	(32.8)	–	57.4	1.0	7.4	0.2	1.2	(67.2)	60	(888)
Period III 1600–2000 hrs	Adult	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	A	–	5.3	–	2.0	–	10.9	(18.2)	42.8	10.0	11.6	17.4	–	–	(81.8)	55	(1090)
	Adult	–	51.3	8.3	0.2	–	–	(59.8)	–	21.1	3.7	9.5	5.7	0.2	(40.2)	38	(436)
	B	1.6	51.5	6.2	2.8	0.4	6.0	(68.5)	–	18.3	7.5	5.7	t	–	(31.5)	115	(1883)
	Adult	–	20.7	0.9	0.9	–	–	(22.5)	–	66.7	5.4	4.5	0.9	–	(77.5)	12	(111)
	C	–	36.2	2.2	–	1.3	–	(39.7)	–	45.7	10.6	4.0	–	–	(60.3)	36	(480)

F* = fly catching, P = pecking, D = diving, HN = extended neck, T = tip, B = begging, S = sleeping, L = locomotion, PR = preening, R = resting, AG = aggression, A = alert.
No data available for Adults in Period III.

during the remainder of the day (Table 3). As the young mature, the attendant adults spent less time in mutual feeding bouts. More of their time was spent swimming and in "patrolling" feeding and resting areas (*sensu* Gullion 1953).

Other activities

Non-feeding activities of young Coots, such as sleeping, swimming, preening and resting, appeared bimodal (Table 3). These behaviours decreased around mid-day and also as the birds grew. Only Class A birds were recorded sleeping. In addition, resting and plumage maintenance occurred more often in these young than in the other two classes. When rest (sleeping and resting) and locomotion are compared, it is obvious that the latter activity increased with age while rest decreased with age and time of day. During the rapid growth phase, Class B, the young spent very little time at rest with the majority of their time directed toward feeding (Table 3). Very little intraspecific aggression occurred except between the young of Class A and B during feeding bouts with their parents. Aggression in Class C was mainly interspecific, similar to that of post-breeding adults where disputes occurred with both dabbling and diving ducks.

Biological costs

Adults, either singly or as a pair, looked after a varying number of young. The average size (± standard deviation) of a Coot brood was 5.35±1.8 young (n=26, range 1–9 young). Rarely more than four young were observed with a single parent; one adult, usually the female, attended to an average of 4.4±1.7 Class A chicks (n=10, range 3–9) while the other adult looked after 3±1.5 chicks (n=7, range 1–4). Class B broods averaged 6.1±0.7 chicks (n=9, range 5–7) while 4.5±2.3 chicks comprised a Class C brood (n=4, range 2–7). In the two older classes, one adult attended on average four young while three or less young accompanied the other adult.

The daily estimates of the time energy budget for Class A, B and C Coot ranged from 270 to 870 kJ day^{-1}, that of the daily energy budget from 301 to 881 kJ day^{-1} (Table 4). Class A young were the most competitive, Class C the least, they expended 0.6 to 0.2 kJ day^{-1} on aggressive interaction. Energy expended on swimming increased from 37 kJ day^{-1} for Class A young to 307 kJ day^{-1} by Class C Coots. Small errors in time-budget measurements contributed to insignificant differences between time and daily energy budgets estimates (x^2=3.561, df=1, P<0.10, Table 4).

The Iowa adult activity data of Ryan and Dinsmore (1979) was averaged to provide energy estimates. Their study focused only on adults, adults without young being incorporated into the time-budgets, and this resulted in a different energy estimate (Table 4). Adult Coots from Iowa expended 935 kJ day^{-1} while Saskatchewan adults expended 886 kJ day^{-1}.

Overall, adults expended an average 65 kJ day^{-1} feeding young, which was similar to the results presented by Ryan and Dins-

Table 4. Estimates of time energy budget (TEB), daily energy budget (DEB) and estimates of energy expenditure on foraging by young and adult American Coots from the present study compared, for adults, with results from Iowa (Ryan and Dinsmore 1979). EM = Maintenance energy.

	Energy Expenditure (kJ bird^{-1} day^{-1} ± standard deviation)		
Coots	Time Energy Budget (TEB)	Daily Energy Budget (DEB)	Foraging
Adults:			
Saskatchewan (a)	886	1010	242
Iowa (a)	935	962	490
Young:			
Class A	270±84	301±156	81
Class B	635±88	623±162	332
Class C	870±97	881±182	182

a. TEB Sask. Σ (cost × %activity × %day 0.667 (& 0.333 night) × EM)
TEB Iowa Σ (cost × %activity × %day 0.625 (& 0.375 night) × EM)

more (1979). However, parental expenditure was 105 kJ day^{-1} for feeding Class A young, declined to 18 kJ day^{-1} for Class B young and was effectively zero for Class C birds. Saskatchewan Coots expended 253 kJ day^{-1} on locomotive activity compared to 39 kJ day^{-1} by adult birds in Iowa. The costs vary from no expenditure on alert behaviour in the presence of Class C young to 1 and 2 kJ day^{-1} on Class A and B young, respectively. Adults spent an average of 55 kJ day^{-1} defending Class B young compared to 30 kJ day^{-1} on Class A and 19 kJ day^{-1} on Class C.

Discussion

Diet

North American studies (Jones 1940; Sooter 1941; Fitzner *et al.* 1980) infer that a progression from a varied to a limited invertebrate diet might occur as the young Coots mature. Jones (1940) found that juvenile Coots ate 46.6% animal food, and Sooter (1941) found that they ate 25%, but neither study provided an indication of diet change with the age of the young. In Washington State, Coots up to 120 days old contained an average of 21% animal matter, which led Fitzner *et al.* (1980) to suggest their values very probably underestimated the importance of invertebrates to Coots up to 30 days old.

European studies on *Fulica atra* such as those of Horsfall (1984a, b) have shown that very young Coots (<30 days old) require large amounts of animal protein. The percent animal matter component in the diet of young European Coots appears to be similar to that reported for its North American congener. For instance, in Latvia, Blums (1973) found young and adults ate 32.1% animal matter, while in Poland intake by young of animal food averaged 43.1% (Borowiec 1975). In contrast, Hurter (1972) recorded 4–21 day old Coots on Lake Sempach, Switzerland, feeding primarily on floating and epiphytic algae and the young shoots of *Phragmites* sp.. Again, nestling and young Coots collected in England by Collinge (1936) contained fragments of insects and molluscs but the main diet was plant material.

This study indicates that the very young, Class A, do have a very high intake of animal protein which declines as the young mature. The invertebrates eaten by Class A Coots contain most of the essential amino acids required for body and plumage development (Sugden 1973; Driver *et al.* 1974). This finding supports the inference of Fitzner *et al.* (1980) that young Coots have a high protein requirement.

The aquatic invertebrates taken by young North American and European Coots are very similar. They selected damsel and dragon fly naiads, adult and larval beetles, hemipterans and caddisfly larvae. The European congener frequently ate pelecypods while gastropods were the mollusca most commonly taken by young North American Coots (Jones 1940; Sooter 1941).

Lepidoptera larvae, insect egg masses and leech cocoons represent foods taken inadvertently with preferred animal foods associated with aquatic marcophytes, such as damselfly nymphs, coroxids, waterboatmen and caddisfly larvae. They may also represent items taken by accident when the young feed on aquatic vegetation; moth larvae living within the stems of aquatic plants, leech cocoons and egg masses (Chironomidae, Trichoptera) laid on the underside of leaves.

Grit

Although Borowiec (1975) did not analyse grit consumption by age the amounts of grit he recorded were similar to the present results for Class B and C young. The Coots in Poland which ate <10 g plant material averaged 2.68 g grit, while those with stomach contents of >10 g plant material averaged 5.09 g grit. In this study the amount of grit increased as the young grew paralleling increased intake of more fibrous plant material. The ingested grit provides for optimum digestion because it increased the motility and grinding action of the gizzard, and enhanced digestibility of coarse and fibrous foods in the remainder of the alimentary tract (Sturkie 1979).

Foraging and other behaviours

The pattern of foraging varied with age as well as with the time of day for the young Coots. The youngest, although attempting a variety of methods to obtain food, primarily used two techniques, pecking and begging, and they occurred with similar frequency. Pecking, although effective in grasping soft and fixed vegetation, appeared ineffective in Class A young for the capture of aquatic invertebrates <15 mm long when compared to the size of food items taken by the older classes. Also very young birds may not yet have learned to handle these prey items and begging was a more productive means of acquiring them.

In young Coots, there are three potential benefits to begging invertebrates from adult birds. First, sitting still and receiving prey rather than actively pursuing them is time efficient and has a low energy cost. Second, it assures the young of a continual source of food rich in essential amino acids necessary for rapid growth. Third, it may introduce them to diving, as both parents dive in front of the begging Class A young. Initially, the adults present the captured invertebrates to Class A young, then they drop dead invertebrates on the water surface in front of the young for easy retrieval, and finally dive without food presentation. On several occasions, food obtained by the adult during "demonstration" dives was dropped in front of the young, retrieved and eaten by the adults while the young watched. Begging behaviour gradually declined by the fifth week as adult diving associated with begging decreased and the diving frequency of young increased.

Biological costs

Energy budgets increase as the young grow (Table 4). During the first 4–5 weeks, when 50–60% of the total body weight is attained (Visser 1974), much of the daily energy requirement is directed towards growth and body heat maintenance (Penney and Bailey 1970). To obtain sufficient energy, the free feeding by Class A young, and to a lesser degree by Class B young, was supplemented by parental feeding, with daily energy expended on begging averaging 36 and 18 kJ respectively. For Class C it was only 0.2 kJ. A portion of the energy which the young might have been spent on body heat maintenance is provided by parents while brooding young on nesting platforms. The high energy expenditure on feeding by Class B young corresponds to the period when large amounts of energy are channelled into feather production as well as to maintenance. With growth there is a deposition of fatty tissue, a high energy tissue, which must represent a diet adjustment by young (Table 1) and a change in feeding cost (Tables 3 and 4).

The involvement of adult birds with their young may be viewed as part of parental investment. Parental investment is any investment made by a parent in one reproductive effort at the expense of its ability to invest in future reproduction (Trivers 1972). Such investment includes commitments of energy and/or time, aggressive interaction, exposure to predators, and a variety of other factors. In this study, part of the investment made by adults is estimated by using the amount of energy expended on specific activities during the brood rearing period. Adults provide Class A, and some Class B, young with food; defend young either by patrolling a "territory" for feeding and resting or by direct aggressive interaction with other birds; and by maintaining an awareness of potential predators.

Most adult aggressive and alert behaviour involved defending the young from other birds entering the "territory" or from potential avian predators. Adult costs vary from no expenditure on alert behaviour in the presence of Class C young to a maximum of 2 kJ day^{-1} when attending younger Coots. Adults spent 55 kJ day^{-1} in aggressive defence of Class B young, who appeared to use more of the wetland than Class A birds. This increased the demands on adults to ward off potential aggressors.

Ryan and Dinsmore (1979) suggest that locomotion is a form of territorial advertisement which serves as a means of territorial defence. The degree of trespassing was very low while the territory owners were visible. They concluded that both sexes, through their locomotive activities, expend a considerable amount of energy on territorial defence. Adult Coots in Saskatchewan appear to expend far more energy (214 kJ day^{-1} more) providing a safe feeding and resting area for their young than those in Iowa.

The investment by adults in their offspring during the brood rearing period which includes feeding young, defence of feeding and loafing sites, and a vigil against predators amounts to an average daily expenditure of approximately 380 kJ day^{-1}. This cost ignores energy expended brooding the young on the nesting platform and the associated costs of defending the young there during the night. This study may have underestimated the time adults spend feeding themselves. Swimming activity by adults may involve foraging which was not recorded. Nonetheless the maintenance of young as an investment is a near maximum cost to the parent attending an average of four chicks. An increase in the number of chicks beyond this number could mean a detrimental cost to the adult where its welfare would be impaired over three to four weeks. It could also result in reduced growth of some of the chicks due to reduced attendance by the adult or to increased chick mortality through predation or attack because of insufficient attention by the parent.

Acknowledgements

I wish to thank Bob Clark for his encouragement and statistical advice. Lawson Sugden assisted in the formative portion of this project. A special thanks to Stuart Keys and Moray Lewis for the many hours they spent in the field and Gerry Beyersbergen for his assistance in the laboratory. I thank Hamilton Greenwood, D.J. Nieman and R.G. Clark for their discussion and review of the manuscript.

Summary

Young Coots became herbivorous with age and their dependence on adults for food declined as they grew. Adult involvement changed from providing food and shelter to merely providing a secure area for the young to forage. Young Coots less than 30 days old ate 84% animal matter; by 60 days of age the amount had declined to 21%. When 30–59 days old, they spent 53% (332 kJ day^{-1}) of their time feeding of which 5.5% was spent begging food from adults. This compared to 30% (81 kJ day^{-1}) for young Coots <30 days old who spent 44% of their foraging time begging. The dominant animal food item was insects. The average energy cost for daily activities of the three age classes calculated from time-budget studies ranged from 270 to 870 kJ day^{-1}. By the time the young were 60 days old (Class C) their feeding and other behavioural activities were very similar to adult birds.

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