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The diet of Grey Herons *Ardea cinerea* breeding at Loch Leven, Scotland, and the importance of their predation on ducklings

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Regurgitations from nestling Grey Herons *Ardea cinerea* at Loch Leven, Scotland, April–July 1981–83, contained mainly three types of prey: perch, brown trout and ducklings. The diet varied markedly through the season but not between years. As the heron breeding season progressed, perch occurred in fewer regurgitations and ducklings in more. There was no seasonal variation in the occurrence of brown trout. Regular collections of duckling down from the heronry suggested that the consumption of ducklings peaked in early June. The ducklings taken by herons were less than 10 days old, Mallard ducklings predominating before mid June and Tufted ducklings later. Most ducklings were taken by only a few herons: those that bred earliest and which initially fed their young on perch. Ducklings became a major part of their diet in the late nestling period and broods fed on ducklings fledged no more or fewer young than others. Herons feeding their young on brown trout took ducklings rarely, if ever. It is argued that variation in the contents of regurgitations resulted from three interacting variables; the type of feeding habitat used by individual Grey Herons, the date at which they bred and the date that regurgitations were produced by their nestlings. The numbers of ducklings taken by herons were calculated to be about 230 in 1981 and 291 in 1982, about 5% of Mallard and 3% of Tufted ducklings estimated to have hatched annually. Assuming herons continued to consume ducklings at the same rate after their young had dispersed, the figures for Tufted ducklings would be higher but still only about 4% in 1981 and 6% in 1982. Compared with total duckling losses of over 75%, predation by Grey Herons was minor and did not affect duckling production in the years concerned.

Introduction

Grey Herons *Ardea cinerea* eat mainly fish but occasionally take birds, mammals and invertebrates (Cramp & Simmons 1977). Prey is swallowed whole but digestion is so efficient that only a creamy grey paste is present in faeces. Indigestible elements, predominantly chitin, fur, or feathers, but also some vegetable material and occasional artifacts (e.g. nylon and fish hooks), are cast up in oral pellets (Hibbert-Ware 1940, Lowe 1954).

The diet of Grey Herons has been investigated using several techniques though none has proved universally adequate, mainly due to small sample size and bias:

(i) Herons have been watched feeding and their prey identified before being swallowed (Cook 1978, Geiger 1984, Richner 1986). This method provides data on diet related to specific times and sites but is heavily biased towards situations where the birds are easily observed and towards prey that are large or easily identified. The sizes of all prey are only poorly estimated (Bayer 1985).

(ii) The stomach contents of dead herons have been used to describe the diet of full-grown birds (Florence 1912, 1914, Müller 1984). The main problems with this method are that samples are necessarily small, up to a third of stomachs are empty and the remainder vary in the state of digestion of their contents.

(iii) The diet during the breeding season has been estimated by examining the food regurgitated by heron nestlings when they are disturbed at the nest (Owen 1955, Moser 1986). This technique can provide large samples of relatively unbiased material but is mainly restricted to May and June. Also such samples are not necessarily representative of the whole heron population because non-breeders and failed breeders provide no material, while nestlings which are short of food seem unwilling or unable to regurgitate. Moreover the items regurgitated by very small nestlings may not be representative of the diet of their parents if small young are fed selectively on small items, as suggested by Moser (1986).

(iv) A fourth method used to investigate diet is by analysis of undigested remains in oral pellets (Hewson & Hancox 1979, Giles 1981, Draulans *et al.* 1987). On a local basis the whole heron population can be sampled throughout the year provided that pellets can be recovered from all roosting places or nests. The contents of pellets do not reflect the whole diet because fish remains are almost absent. Nevertheless, the feathers and fur present are most, if not all, of that consumed (Milstein, Prestt & Bell 1970) because the gizzard has little grinding action (Hibbert-Ware 1940) and there is little opportunity for keratinous material to be fragmented and passed down the gut. This means that the intake of mammals and birds can be estimated by comparing the mass of feather and fur in pellets with the mass of such material borne by bird and mammal prey.

We studied the diet of breeding Grey Herons in Scotland, mainly using regurgitations from nestlings. Samples from seven different areas (Fig. 1) showed that ducklings were important only at one colony, near Loch Leven, Tayside. The present study reports the diet of herons at the latter colony and assesses the impact of heron predation on the duckling population there.

Study area and methods

Loch Leven is a large shallow eutrophic loch and has long held the largest concentration of nesting ducks in Britain (Allison, Newton & Campbell 1974). Just over 1000 pairs of ducks breed there, predominantly Tufted Ducks *Aythya fuligula* (500–650 pairs) and Mallard *Anas platyrhynchos* (400–450 pairs), most of which breed on St Serf's Island. A census of duck nests in 1981 showed little change from counts in 1966–71 (Wright 1986). Using the 1981 figures combined with the published data on seasonal trends in egg-laying, clutch-size and hatching success (Newton & Campbell 1975) we calculated about 7500 ducklings hatch between the second week of April and the first week of August (Fig. 2), with peaks in May (Mallard) and late June (Tufted Duck).

Herons ceased breeding at Loch Leven about 1900 and nesting did not start again until 1972 (Allison *et al.* 1974). As in other parts of Scotland (Marquiss 1989) numbers increased to a peak (25 pairs) in 1982, then fell (to 19 pairs) by 1985 (Fig. 3). The three years reported in this study are those when heron numbers were highest and, hence, when their impact on ducklings might have been expected to be greatest.

Collection of material

Pellets were collected at two-weekly intervals, from March to mid-August, in both 1981 and 1982; searches included all known roosts and every nest tree. Some pellets were from nests but most came from the ground below. It was easy to distinguish pellets from different nests, which were usually well separated, while in two cases where adjacent nests were close, no pellets were found below. Only a few

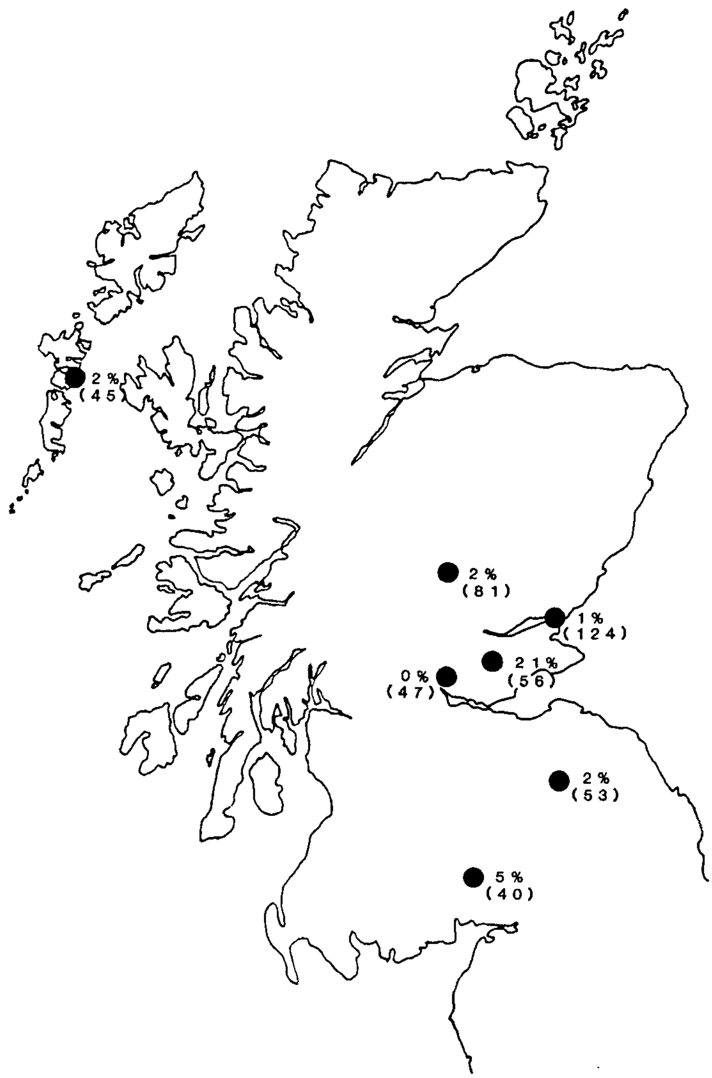

Figure 1. The percentage frequency of ducklings in regurgitations (*n*) from Grey Heron nestlings, in seven parts of Scotland.

pellets were found below trees used as perches and in a field adjacent to the colony, where both breeding and non-breeding herons spent time roosting and preening. On each visit to the heronry some trees were climbed, so that nests were inspected about once a month to record clutch-size, hatching and fledging success, and to ring the young. On such visits young herons usually regurgitated their most recent meal, from which items were usually identified, measured and returned to the young but on some occasions unidentified material was removed for further examination. In 1983 timber felling disrupted one edge of the colony and 4 of the 21 pairs nested on islands in the loch, where visits and pellet collections were less frequent.

Laboratory analyses

Pellets were broken up, separated into down, feathers and hair from different species (Day 1966, Fjeldså

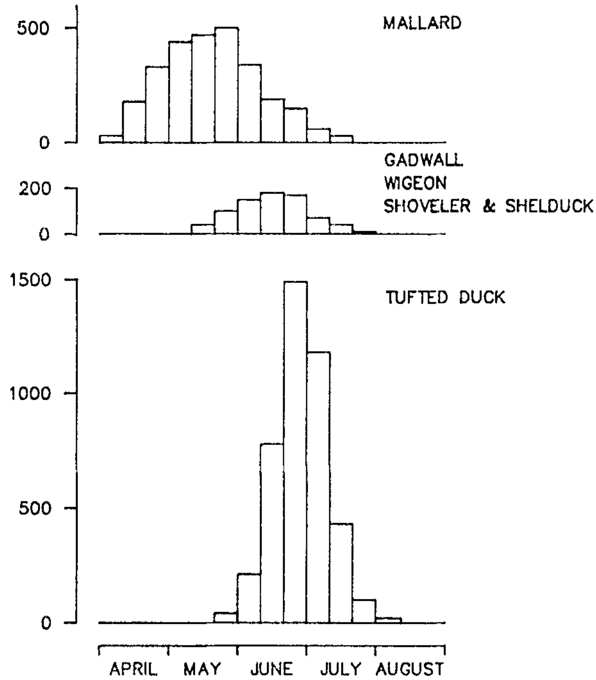

Figure 2. Numbers of newly hatched ducklings at Loch Leven in 10-day intervals throughout the breeding season, calculated by applying the seasonal trends in egg-laying, clutch-size and hatching success (Newton & Campbell 1975) to the census of duck nests in 1981 (Wright 1986).

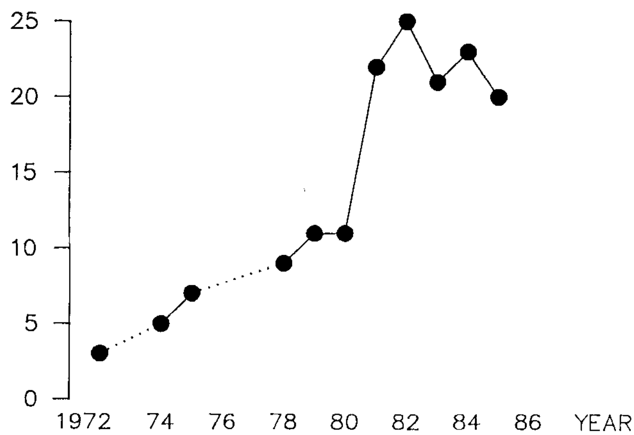

Figure 3. Numbers of Grey Heron's nests at Loch Leven, 1972–85.

1977), and all down was dried and weighed. We were only able to distinguish duckling species where feet or bill sheaths were present.

In total, the contents of 56 nestling regurgitations were examined; 23 in 1981, 24 in 1982 and 9 in 1983. Whole items were identified and measured using length from snout to tail-fork for fish (Maitland 1972), hind-foot or head- and body-length for mammals (Southern 1964) and tarsus-length for birds (Cramp & Simmons 1977). Some fish were part-digested so their vertebrae were washed in a sieve, identified (Webb 1976) and measured. The length of the fish was then calculated from the size of the vertebrae using published relationships (Wise 1980). The masses of fish were estimated using length/mass relationships for trout *Salmo trutta* (Clelland 1980), perch *Perca fluviatilis* (Le Cren 1951) and eels *Anguilla anguilla* (Tesch 1977). The masses of mammals were taken from Southern (1964) and frogs *Rana temporaria* from Frazer (1983). Sticklebacks *Gasterosteus aculeatus* weighed on average 1·8 g and great diving beetles *Dytiscus marginalis* 0·9 g.

We estimated the sizes of ducklings that herons consumed by measuring tarsi recovered from regurgitations. We wished to calculate the body mass of these ducklings and the mass of their down, so we used relationships derived from measurements of 15 dead ducklings between hatching and 10 days of age. They were weighed, measured and their down was plucked, dried and weighed.

Results

The diet of herons at Loch Leven

The diet was diverse, with at least 14 species of vertebrates including fish, mammals and downy chicks (Table 1), but perch, trout and ducklings accounted for two-thirds of items and almost three-quarters of the biomass consumed. Other items were too infrequent or too small to be important. Perch was the most important species because it was frequent and individually large, comprising mainly fish of 16–22 cm length and more than 100 g mass (Fig. 4). The median estimated mass of individual

Table 1. *The contents of regurgitations from Grey Heron nestlings at Loch Leven, 1981–83*

Prey	Number of regurgitations where present ($n = 56$)	Frequency of items ($n = 128$)	Percent biomass ($\Sigma = 11{\cdot}98$ kg)
Oystercatcher *Haematopus ostralegus* (chick)	1	1	trace
Black-headed Gull *Larus ridibundus* (chick)	2	3	0·1
Mallard *Anas platyrhynchos* (duckling)	8	12	9·1
Tufted Duck *Aythya fuligula* (duckling)	5	11	5·2
Water vole *Arvicola terrestris*	3	4	7·5
Brown rat *Rattus norvegicus*	3	3	5·6
Mole *Talpa europaea*	1	1	0·9
Water shrew *Neomys fodiens bicolor*	1	1	0·2
Stickleback *Gasterosteus aculeatus*	4	16	0·2
Eel *Anguilla anguilla*	2	4	5·3
Perch *Perca fluviatilis*	25	35	48·3
Brown trout *Salmo trutta*	12	27	10·1
Rainbow trout *Salmo gairdneri*	1	1	1·7
Unidentified fish species	4	6	5·5
Frog *Rana temporaria*	1	1	0·3
Great diving beetle *Dytiscus marginalis*	2	2	trace

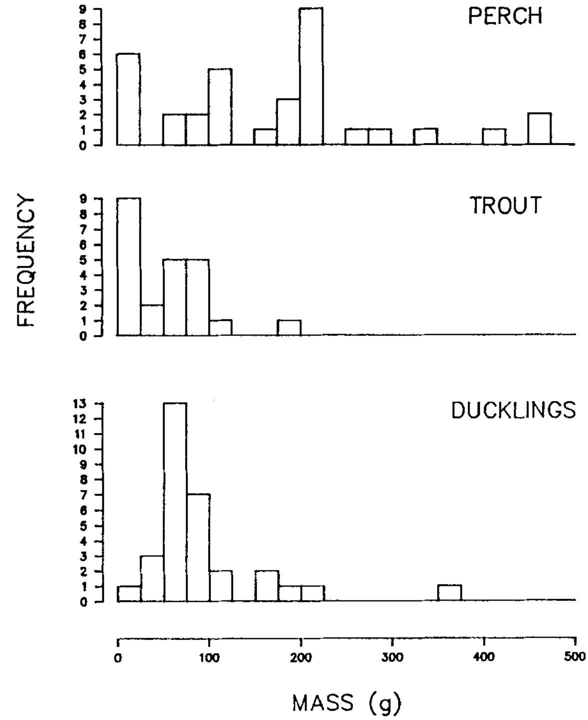

Figure 4. Mass-frequency distribution of the major prey taken by Grey Herons at Loch Leven, 1981–83.

perch in the diet was 187 g compared with the median mass of 71 g for ducklings and 50 g for trout. There was no evidence that smaller nestlings (< 20 days old) were fed selectively on smaller prey (< 50 g, Moser 1986). Only two of nine regurgitations from young nestlings contained such small items, compared with 18 of 44 regurgitations from older nestlings ($\chi^2_4 = 0{\cdot}45$, n.s.). Small nestlings often regurgitated pieces from fish that were too large for them to have swallowed whole. Presumably these fish had been predigested by adult herons before being fed in pieces to their young.

Separate items within regurgitations did not occur independently of one another. A perch was more likely, and a trout less likely, to be regurgitated on its own than would be expected by chance and there was a strong tendency for items of the same species to occur together (Table 2). This was particularly so for trout, which also never occurred in the same regurgitations as ducklings and only rarely with other prey types. This meant that when searching for variation in the diet (e.g. between seasons or years) we had to use regurgitations and not individual items as the units of comparison.

There was no suggestion of any major differences in diet between years. Too few regurgitations were examined in 1983 to detect differences but the four main prey types occurred with similar frequencies in 1981 and 1982 ($\chi^2_4 = 2{\cdot}74$, n.s.). There was, however, strong seasonal variation, with perch decreasing and ducklings increasing as the season progressed (Table 3). There was no seasonal trend in the occurrence of trout but a marginal tendency for other species collectively to occur more frequently later on.

Table 2. *The frequency of associations between items of four different prey types within regurgitations*

	Single item	Perch	Trout	Duckling	'Other'
Perch	16	20	—	—	—
Trout	3	9	41	—	—
Duckling	5	14	0	13	—
'Other'	6	5	7	36	80

Note: The frequency of associations between items within regurgitations was different to what would have been expected had the four prey types occurred at random and independently of one another ($\chi^2_{12}=270$, $P<0{\cdot}001$).

Table 3. *Seasonal variation in the frequency of four prey types in regurgitations of Grey Heron nestlings*

Date	Number of regurgitations examined	Number containing			
		Perch	Trout	Duckling	'Other'
April 1–15	2	2	0	0	0
April 16–30	4	3	0	1	0
May 1–15	13	8	2	1	2
May 16–31	11	4	4	3	4
June 1–15	19	8	3	5	8
June 16–30	4	1	3	0	1
July 1–15	1	0	0	1	0
July 16–31	2	0	0	2	1

Note: Using Snedecor & Cochran's test for a linear trend in proportions, there was a significant seasonal decrease in perch ($z=2{\cdot}74$, $P=0{\cdot}006$), an increase in ducklings ($z=2{\cdot}19$, $P=0{\cdot}029$), no trend for trout ($z=1{\cdot}03$, $P=0{\cdot}303$) but a marginal tendency for an increase in 'other' species ($z=1{\cdot}70$, $P=0{\cdot}089$).

The seasonal trend in the predation of ducklings, evident in regurgitations, was much more pronounced in the production of pelleted down. The mass of duckling down collected from the whole heronry in two-weekly periods increased through May to a peak in early June and then decreased during July (Fig. 5).

Species and size of ducklings in the diet

Thirteen regurgitations and nine pellets contained remains which could be identified positively as Mallard or Tufted ducklings. Tufted ducklings were not present in material collected before mid-May, whilst Mallard ducklings were not found in material collected in July–August. In the intervening period, the ratio of Mallard to Tufted ducklings decreased gradually from 5 : 1, to 3 : 2, then 2 : 3 in two-weekly intervals. Other species of ducklings were not identified in our material and

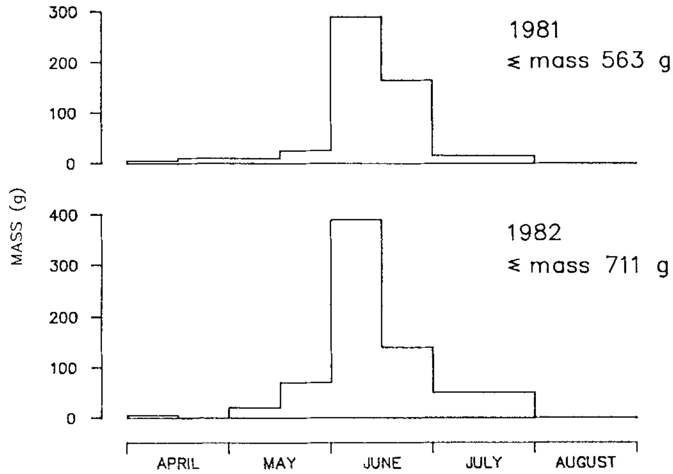

Figure 5. Total mass (g) of duckling down from Grey Heron pellets at the Loch Leven heronry in two-weekly periods, 1981–82.

presumably were taken infrequently because they were relatively scarce at Loch Leven.

The tarsi of 15 Mallard and 17 Tufted ducklings were recovered intact. Tufted duckling tarsi averaged 22·9 mm ± 0·5 (s.e.) with the largest at 26 mm, while Mallard tarsi averaged 28·1 mm ± 1·26 (s.e.) with one much larger than the rest at 40 mm. Tufted ducklings are smaller than Mallard of the same age and have much shorter tarsi (Kear 1970). Most ducklings must have been only a few days old when eaten and none was over about 10 days of age.

The numbers of ducklings consumed by herons

The relationship between the length of a duckling tarsus (t) and the mass of its down (M_d) were calculated as:

$$\sqrt{M_d} = 0{\cdot}091t - 0{\cdot}910 \text{ (Mallard)}$$
$$\sqrt{M_d} = 0{\cdot}089t - 0{\cdot}638 \text{ (Tufted Duck)}$$

Using these equations and the measurements of all tarsi recovered intact from regurgitations, we calculated the average mass of down on ducklings consumed by herons as 1·99 ± 0·11 g (s.e.) for Tufted ducklings and 2·90 ± 0·42 g (s.e.) for Mallard. For each month from April to August in 1981 and 1982, we had estimates of the total mass of duckling down in heron pellets (Fig. 5), the ratio of Mallard to Tufted ducklings in their diet, and the average mass of down per duckling, from which we calculated the numbers of ducklings consumed per month throughout both breeding seasons (Table 4).

Assuming that the seasonal trends in hatching success, reported by Newton & Campbell (1975), still applied in 1981 and 1982, we expressed the number of ducklings taken by herons as a proportion of those which hatched. Such predation 'rates' varied seasonally; an increase in the numbers taken in June meant predation on Mallard was heaviest then, although in proportional terms the greatest toll on Tufted ducklings was on those few hatching in late May (Table 4). The number of Mallard ducklings taken over the whole breeding season was about 5% (1981) or 6%

Table 4. *The estimated numbers of Mallard and Tufted ducklings hatched (from Fig. 1) at Loch Leven and the calculated numbers taken by Grey Herons from April to August, 1981 and 1982. The figures in parentheses are minima and maxima, derived from the 95% confidence limits around the estimate of mean mass of down on ducklings consumed by herons*

	Mallard			Tufted ducklings		
		Number taken			Number taken	
Month	Number hatched	1981	1982	Number hatched	1981	1982
April	490	3 (2–4)	1	0	0	0
May	1421	14 (11–19)	30 (23–42)	36	2 (2–3)	4 (3–6)
June	652	102 (83–131)	114 (93–147)	2478	93 (76–119)	97 (80–125)
July	72	0	0	1670	15 (13–16)	45 (41–51)
August	0	0	0	8	1	0
Annual total	2635	119 (96–154)	145 (117–190)	4192	111 (92–139)	146 (124–182)
Numbers as % of those hatched		5 (4–6)	6 (4–7)		3 (2–3)	3 (3–4)

(1982) of those calculated to have hatched. The number of Tufted ducklings taken was about 3% of those hatched. The maximum figures, derived from the 95% confidence limits, were 7% for Mallard and 4% for Tufted ducklings in 1982.

The importance of ducklings to herons

The weight of duckling down recovered from the vicinity of individual heron nests over the breeding season varied from zero to 276·7 g. Although duckling down was recovered from 49 of 68 nesting trees over the three years, 95% came from only a third of these trees. In each year, only two or three nests accounted for two-thirds of all the down collected. Evidently most ducklings were taken by a few herons. The frequency of ducklings in regurgitations from individual nests was in broad agreement with the results from down collections (Table 5). From those five nests where down was most abundant, ducklings were present in about two-thirds of regurgitations and contributed about 34% to their biomass. These regurgitations also had the highest frequency of perch, but trout were absent. Trout were found most frequently in material from nest trees where duckling remains were absent.

Ducklings were most frequently regurgitated by the broods of herons that bred early and there was a significant relationship between the total weight of down recovered from a nest and the date on which young hatched (Table 5). The associations in Table 5 also suggest that herons breeding later in the year were more likely to feed their young on trout but an analysis of regurgitation contents on hatching date showed only a marginal relationship, if any (Snedecor & Cochran's test for trends in linear proportions: $z = 1{\cdot}63$; $P = 0{\cdot}103$). There was, however, a strong tendency for those herons which fed their young on perch to be early breeders ($z = 2{\cdot}42$; $P = 0{\cdot}008$). Although herons feeding their young on ducklings and perch bred earlier, they did not produce significantly more or fewer fledged young than others (Table 5). An additional analysis including all broods for which there were regurgitations showed no significant differences in the mean sizes of broods regurgitating different prey types (Table 6).

Table 5. *The diet and breeding performance of Grey Herons taking differing numbers of ducklings (data from all nests, 1981–83)*

	Mass (g) of down per nest			
	0–0·1	1·1–10·0	10·1–100·0	≥100
Number of nests	25	23	15	5
Number of regurgitations	13	14	14	15
Number of items	31	31	20	46
Ducklings in the diet				
% regurgitations with ducklings	0	7·1	14·3	66·7
% items	0	3·2	10·0	41·3
% biomass	0	2·9	5·3	33·6
Other major prey				
% regurgitations with perch	23·1	50·0	50·0	60·0
% regurgitations with trout	61·5	21·4	7·1	0·0
% regurgitations with 'other' prey	30·8	35·7	28·6	20·0
Breeding performance (mean ± s.e.)				
Hatching date (from 1 April)	22·8 ± 2·6	17·8 ± 2·5	16·6 ± 3·7	8·6 ± 2·9
Fledged brood-size	1·81 ± 0·22	1·86 ± 0·21	1·85 ± 0·19	2·00 ± 0·32

Note: The linear regression of hatching date (y) on the production of duckling down (x) was significant,

$$y = 26{\cdot}19 - 0{\cdot}070x \ (t_{57} = -2{\cdot}214,\ P < 0{\cdot}05)$$

but not that of fledged brood-size ($t_{57} = 0{\cdot}244$, n.s.).

Table 6. *Fledged brood sizes for Grey Heron nestlings regurgitating different types of prey (data from all nests 1981–83)*

	Perch	Ducklings	Trout	'Other'
Mean ± s.e. (n)	2·16 ± 0·16 (19)	1·89 ± 0·20 (9)	2·67 ± 0·29 (9)	2·19 ± 0·16 (16)

Note: There was no difference in the mean brood-sizes between years (two-way ANOVA, $F_{2,32} = 0{\cdot}488$ n.s.) and no difference in the sizes of broods regurgitating different prey types in a single year, 1982 (two-way ANOVA, $F_{3,17} = 1{\cdot}904$ n.s.) nor in data from all years combined (two-way ANOVA, $F_{3,49} = 1{\cdot}961$ n.s.).

The production of duckling down in pellets was plotted against the stage of the heron's breeding cycle in individual nests, to see whether peak duckling consumption coincided with the time at which the young herons required most food, i.e. between 2½ and 5 weeks of age, at the upper end of the linear stage of growth (Owen 1960). We used data from two nests in 1981 and three in 1982, which accounted for more than two-thirds of the down collected in these years.

The peak regurgitation of duckling down occurred at 6–8 weeks old (Fig. 6), i.e.

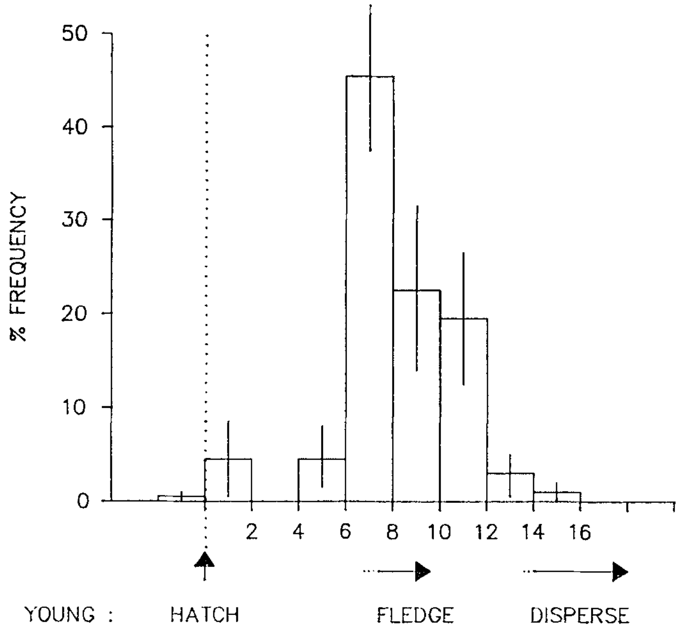

Figure 6. Mean percentage frequency (±s.e.) of duckling down produced by Grey Herons during incubation and throughout the nestling period. Data from the two nests in 1981 and three nests in 1982, which accounted for more than two-thirds of the down collected in these years.

about a week before heron chicks were expected to fledge and well after the period of maximum food intake. Before the chicks were 6 weeks old, perch occurred in four out of five regurgitations but ducklings in only one. After 6 weeks, both perch and ducklings occurred with the same frequency, in six of eight regurgitates. The small amount of information available suggests that perch were important in the diet when the nestlings' food requirement was greatest and ducklings increased in the diet well afterwards.

Discussion

Variation in the diet

Only with the use of pellets could we sample the breeding season diet systematically, for all herons, throughout the breeding season. The contents of pellets showed that there was large variation, at least in the amount of ducklings taken, between pairs and with season but with a relatively small difference between the two years. Regurgitations gave information on the whole diet but samples were small where they were subdivided to investigate variation between years, seasons or groups of nests. This problem was exacerbated by the lack of independence in the occurrence of items within regurgitations. Unlike other workers (Owen 1960, Moser 1986) we could not merely compare the frequency of items in lumped samples of regurgitations.

Regurgitations were few, and came from only a small segment of the heron population. Although young herons regurgitated at all ages from 1 to 13 weeks, 80%

of our samples came from nestlings aged 2–8 weeks. Thus the seasonal changes we recorded in the contents of regurgitations could have been due either to seasonal trends in the diet of herons, or to the diet of early nesting herons differing from the diet of those nesting later. Our data suggest that both effects occurred. The diet of most early breeding herons did change, from perch in the period of maximum food intake, to ducklings shortly before fledging. Other herons, predominantly those breeding in mid or late season, fed mainly on trout, with no detectable seasonal trends in diet.

One explanation for the variation we found might be that diet is related to the habitat at the feeding sites of individual herons. Feeding habitat around Loch Leven could be broadly categorized as: (i) feeder streams to the loch where brown trout were abundant; (ii) loch edge, particularly at stream inlets where perch, trout and a few ducklings occurred and (iii) the fringes of the loch, particularly on the east side and around St Serf's Island, where both spawning perch and ducklings were abundant in submerged and semi-emergent vegetation.

Perch may have been particularly vulnerable when they came into shallow water to spawn, from late April to late May at Loch Leven (Jones 1982). This could explain their predominance in the diet of herons at this time, with the switch to other items, including ducklings, taking place as perch died or returned to deeper water. In contrast, herons hunting in feeder streams would find trout available throughout the summer.

It is not obvious why herons which fed extensively on ducklings were the earliest of breeders. There was little information on the diet prior to and during laying but one major food was frogs. The unexpanded spawn from gravid frogs littered the heronry at this time. Perhaps feeding sites harbouring a good supply of ducklings were also those which offered the greatest, or earliest, abundance of frogs in March.

It was surprising that so few herons fed on ducklings, which at Loch Leven were abundant and vulnerable. Perhaps breeding Grey Herons do not congregate to exploit local prey abundance, as tentatively discussed by Krebs (1974). A study of feeding Grey Herons during the breeding season, using radio-telemetry, showed that as the season progressed birds became more faithful to specific feeding sites and territorial (Van Vessem & Draulans 1987). By the time ducklings became abundant at Loch Leven most heron nestlings were well-grown. At that stage they required no brooding or guarding by the parents, which might then have been able to defend feeding sites, so preventing the congregation of herons in duckling nursery areas.

The numbers of ducklings taken by Grey Herons at Loch Leven

The total numbers of ducklings consumed could only be estimated accurately if all of the duckling down pelleted by herons was recovered. We assumed that pellets were not deposited at foraging sites, so the down from most ducklings consumed would have been cast up at the heronry or at nearby roosting places. This was probably correct, at least until midsummer, because herons were not seen roosting elsewhere in the area until late June. We thought that even non-breeding birds roosted near the colony because we regularly saw birds in subadult plumage and two individually marked, non-breeding yearlings were seen often in April and May, though not thereafter. This was consistent with detailed studies of radio-telemetered herons elsewhere; Van Vessem & Draulans (1987) found that attendance by non-breeders declined after the majority of young hatched. Had non-breeders at Loch Leven fed on ducklings, their depredations from June onwards would have gone unrecorded. However, they were few and their consumption would have been trivial compared with that of breeders, which themselves probably left the colony before they ceased feeding on ducklings. One early breeding pair which failed and produced a replacement clutch in May 1983, provided large amounts of duckling down up to the end of July. Had this pair bred successfully at their first attempt the young would have dispersed and the adults left the colony by mid July, though the adults might have continued to feed on Loch Leven ducklings whilst casting pellets at roosts elsewhere. If this happened our estimates of the numbers of ducklings taken would be too low, so we recalculated consumption assuming that adult herons continued to feed on ducklings at the same rate, for as long as ducklings were available. Under these circumstances they could have consumed an extra 66 Tufted ducklings in1981 and 102 in 1982. This would have increased the estimates of the proportion taken annually, from 3% (Table 4), to 4% and 6% respectively. Mallard ducklings were not available so late in the season, so their numbers would remain unchanged at 5% and 6% of those hatched.

These figures are crude, because it was unknown how many ducklings hatched in 1981 and 1982. We have assumed the duckling population varied little from year to year and this was probably not so. Nevertheless we are confident that although thousands of ducklings hatched annually, no more than a few hundred were eaten by herons in those years.

Ducklings are difficult to census and only rough estimates of survival to fledging are available at less than 100 Mallard, but up to 500 Tufted ducklings annually (Allison *et al.* 1974, Wright 1986). Clark *et al.* (1987), using radio telemetry, estimated that 570–690 Mallard ducklings survived in 1986. It is not known whether this was an unusual year, but it still suggested enormous losses of over three-quarters of Mallard and Tufted ducklings, most of which occurred within the first week after hatching. Our estimates suggest that Grey Herons consumed only about one in fifteen of these. Large gulls, pike *Esox lucius*, crows, and mustelids also ate ducklings (Allison *et al.* 1974) but in unknown quantities.

High mortality rates have been recorded for small ducklings at other sites where ducks breed in large concentrations. At Mývatn in Iceland, where there are no herons, average mortalities are 47% for surface-feeding ducks and 60% for diving ducks but in some years these reached 73% and 80%, respectively (Bengtson 1972). For most nursery areas in the Ythan estuary in northeast Scotland about two-thirds of Shelducklings *Tadorna tadorna* died (Makepeace & Patterson 1980), and, also on the Ythan, on average about 90% of Eider *Somateria mollissima* ducklings died (Mendenhall & Milne 1985). In these three studies predation by gulls or skuas was an important proximate cause of death though other factors such as cold weather, disturbance (Åhlund & Gøtmark 1989) or strife (Pienkowski & Evans 1982) have been cited as more important than, or predisposing, predation. In one study of Mallard ducklings, where predators were controlled, mortality was still at least 77% and was attributed to poor food supply (Street 1977).

Herons took a small proportion of the ducklings at Loch Leven, and those at a stage (less than ten days old) when mortality was in any case high. Considering the poor survival at Loch Leven (even in the years before herons became common) it seems unlikely that they had any impact upon overall duckling production.

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