The food of Mallard ducklings in a wet gravel quarry, and its relation to duckling survival

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Introduction

The area of flooded gravel quarry habitat is increasing annually and these artificial wetlands could help to replace and, in some cases supplement, natural wetlands, making a significant contribution to the production of indigenous wildfowl species. The W.A.G.B.I.—Wildfowl Trust Gravel Pit Reserve at Sevenoaks, Kent is an example of this. There is, however, a major problem with the rapid establishment of breeding wildfowl populations on very recently restored gravel workings, and this is the unduly high mortality among downy ducklings, especially those of the Mallard *Anas platyrhynchos*. The principal aim of the Game Conservancy's Wildfowl Project is to determine the factors which affect the survival rate of Mallard ducklings so that management plans for new gravel pit reserves can be altered accordingly.

Duckling mortality in the gravel pit study area at Great Linford, Buckinghamshire, has been consistently high, around 77% over the period of the study. This is in a situation where predators, with the exception of Pike *Esox lucius*, are rigorously controlled and where it can be assumed that predation is not the major cause of duckling losses. This paper presents the results of the analyses of the gut contents of 99 wild Mallard ducklings from 0–45 days old which were collected in the study area over four seasons.

The emergence of insects from the reserve was monitored in 1975 and 1976 by the use of insect emergence traps and by sweep netting. Some of the results of this survey are presented, and the availability of adult insects is related to the survival of Mallard ducklings.

The study area

This is a 300 hectare gravel quarry alongside the upper reaches of the Great Ouse river at Great Linford in north Buckinghamshire (Figure 1). A very small proportion of these workings is approximately 37 years old, but the greater part is much more recent, having been excavated in the last 12 years. Most of the study area wetlands are therefore ecologically very immature. There are no extensive areas of shallow water and only about one-quarter of the area of standing water contains an appreciable amount of submerged aquatic macrophytes. In the rest of the quarry these are either restricted by high turbidity or have not yet developed. The bed of all the lakes is composed of a mixture of gravel and clay on an underlying band of blue clay. Only in the older parts of the quarry is there any accumulation of organic sediment.

The Game Conservancy's wildfowl reserve occupies approximately 37 ha of the quarry. It consists of 29 ha of open water from 0·5 to 4·5 m deep plus an 8 ha complex of islands and lagoons 0·5 to 2·5 m deep. This area holds the majority of the breeding wildfowl. The ratio of land to water in the island complex is 3·1:1·0 and there is 0·74 km of shoreline per hectare. The whole quarry is a valuable site for wintering wildfowl but only the Mallard and Tufted Duck *Aythya fuligula* breed in some numbers.

In 1972 the reserve contained virtually no aquatic vegetation and little ground cover. Since then 5·4 km of shoreline in the reserve has been planted with a variety of emergent vegetation, chiefly bur-reed *Sparganium erectum*, reed-grass *Glyceria maxima*, common reed *Phragmites australis*, pond sedge *Carex riparia*, reedmace *Typha latifolia*, and sea club-rush *Scirpus maritimus*. The exclusion of grazing stock led to the rapid establishment of ground cover dominated by the tufted hair grass *Deschampsia caespitosa*, with nettles *Urtica dioica*, docks *Rumex* spp., thistles *Sonchus* and *Cirsium* spp., willow herb *Epilobium* spp., and coltsfoot *Tussilago farfara* as the other main species.

Material and methods

Mallard ducklings were collected (under licence from the Nature Conservancy Coun-

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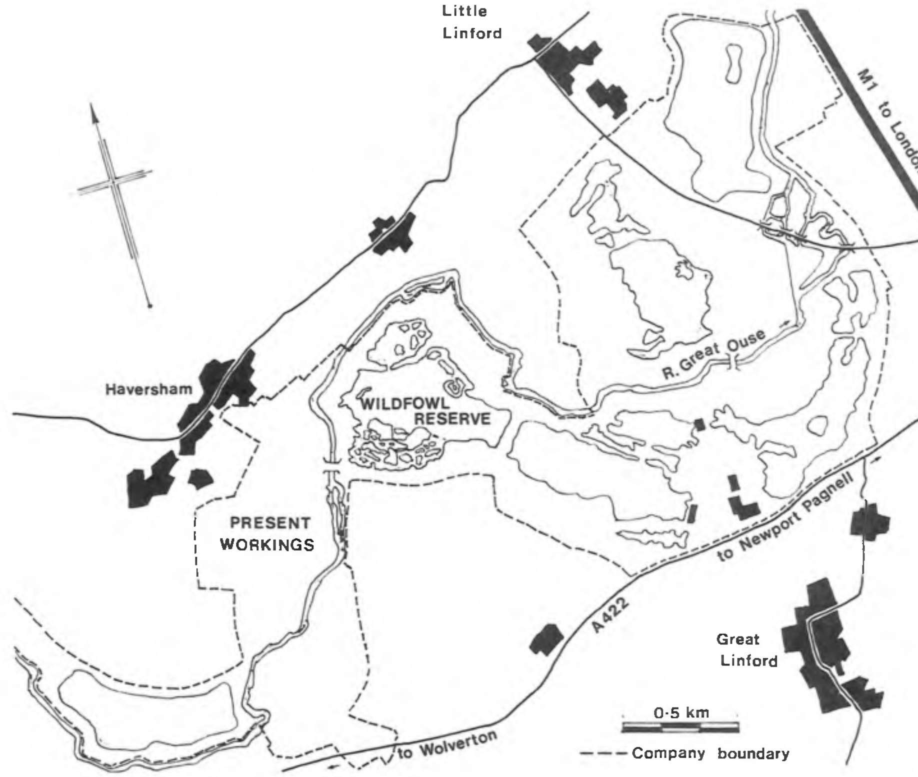

Figure. 1. The Great Linford Gravel Pit study area.

cil) during brood searches conducted at all times of day between March and August. The ducklings were aged by use of plumage characteristics (Southwick 1953) and by comparison of their size with that of the adult female (Hilden 1964). Table 1 shows the numbers and ages of the ducklings collected.

They were stored in a deep-freeze to prevent post-mortem digestion and on thawing, the contents of the oesophagus, proventriculus and gizzard were removed and placed in 70% ethanol for examination. Each food item was counted and identified as far as possible. Where only part of an organism remained the numbers of a particular component part were counted, for example the head cases of Chironomid larvae or the elytra of beetles, and the number of each was divided by the number of such parts possessed by one organism to arrive at the numbers of each organism eaten. Plant food was mainly in the form of seeds, which were usually found entire, but where they were not whole, the number eaten was estimated in a similar manner.

The number of each item found is given as a percentage of the total number of items found, together with their frequency of occurrence, in preference to weights or volumes as these may over-emphasise the importance of bulky or heavy types of food. Other

Table 1. Numbers and ages of the ducklings used for food analysis.

Age class	Ia	Ib	Ic	IIa	IIb	IIc	III
Age in days	1–6	7–12	13–18	19–25	26–35	36–45	46–55
1972	11	1	2	3		6	8
1973	21	29	1	2	2		
1974	5		2	3			
1975	2		1				

workers in this field have also expressed results as numbers of food items found (Bengtson 1975; Chura 1961).

The gizzard contents are included in the analyses despite the fact that they bias the results in favour of the harder, less digestible foods (Swanson & Bartonek 1970). In a large proportion of the sample only the gizzard was found to contain food, and other workers (Chura 1961; Collias & Collias 1963) have also had to use gullet/gizzard contents in this way.

Insect emergence

The emergence of insects from the waters of the study area was monitored in the summers of 1975 and 1976, while at the same time, brood searches were made to assess duckling production and mortality rate.

Between 29th April and 27th June 1975, four insect emergence traps, made to the design of Mundie (in Edmondson & Winberg 1971) were sited as shown in Table 2. Each trap covered an area of 0·25 square metre of water surface. The traps were emptied daily by washing the insect catch out of the inverted trap with a pre-determined volume of water. This method of emptying the trap was estimated to be at best 50% efficient. The catches were stored in 70% alcohol, and were later identified and counted.

In 1976 a different design of trap was used. This was a square, floating box frame covered on the sides with fine nylon gauze and with a transparent perspex lid. These covered 0·5 square metres of water and were found to be more satisfactory than the Mundie Traps. The catch was removed from these traps every second day by means of an entomological aspirator (pooter). This method was found to be about 75% efficient. These traps were sited in the positions shown in Table 3 between 6th May and 20th August 1976.

To obtain an indication of the availability of insects to ducklings feeding on land, three selected 10 metre stretches of waterside vegetation were sampled regularly with an insect sweep net. Each strip was covered by 15 sweeps of the net about an arc of approximately one metre. The vegetation thus sampled was (a) a mixed zone of nettle *Ur-*

Table 2. Position of the Mundie emergence traps; 29th April–27th June 1975.

Trap number	Water depth (metres)	Position	Vegetation and substrate
1	2·0	Sheltered pool in breeding reserve	*Myriophyllum spicatum* *Potamogeton pectinatus* *Elodea canadensis* Silty clay bed
2	1·5	Larger open pool in reserve	No vegetation, gravelly clay bed
3	1·5	As above	As above
4	0·5	Littoral fringe in reserve	*Scirpus maritimus* on gravelly clay

Table 3. Position of the emergence traps; 6th May–30th August 1976.

Trap number	Water depth (metres)	Position	Vegetation and substrate
1 and 2	1·0	Isolated pool in breeding reserve	*Elodea canadensis* *Myriophyllum spicatum* Silty clay bed
3 and 4	1·5	Larger sheltered pool in reserve	Elodea canadensis Silty clay bed
5	0·2	Littoral fringe	*Sparganium erectum* Sandy gravelly soil
6	0·2	Littoral fringe	*Glyceria maxima* Sandy gravelly soil
7	0·2	Littoral fringe	*Carex riparia* Sandy gravelly soil

tica dioica and thistle *Cirsium sp.*; (b) tufted hair grass *Deschampsia caespitosa*; and (c) reed grass *Glyceria maxima.*

Brood searches

In 1974, 1975 and 1976, frequent brood searches were carried out in the study area to enable assessment of the mortality rate among Mallard ducklings to be made. Most searches were made on foot, at varying times of day but covering a similar route each time. Dogs were used to flush broods from areas of dense cover. Individuals in the broods seen were counted and their age was estimated. The number of young, age and location of each brood was recorded and a note made of peculiarities of the plumage of the parent bird if any. Thus a brood seen again at a later date was usually recognizable as a repeat observation.

If the number of nesting females, percentage nest success and the percentage hatch per successful nest was known it would be possible to calculate young to old ratio at hatching. Any subsequent decrease in this ratio would be due to duckling mortality.

Unfortunately the extended nesting season means that the estimation of the number of breeding females from the number of nests found is not possible as the latter would include an unknown proportion of re-nests. Subsequent estimation of the young to old ratio would be extremely difficult as records of the number of adult females seen without young would include 'off duty' females, non-breeders and birds whose nests had failed as well as females which had lost their broods.

Duckling mortality was therefore estimated from the decrease in mean brood size with the age of the brood. This does not take into account those broods which are lost completely and therefore results in a mortality underestimate which could be at least 30% (Ball *et al.* 1975).

The number of broods encountered during one of the regular brood searches were considered to be a reasonable estimate of the duckling population at the time of the search, assuming that the same effort was made in each search. Thus any change in the numbers of broods of different age classes encountered in successive searches was assumed to be indicative of changes in the structure of the duckling population. For example, the reduction in the frequency with which broods of a particular age class were encountered over the period of brood searches probably means that the number of broods of that age class present on the study area decreased. This decrease in the number of broods in each age class with time is due to graduation of the broods into the next age class or to mortality of whole broods. It is thought unlikely that a significant number of the young broods left the study area, despite the considerable mobility of Mallard (Beard 1964), as there is no alternative brood rearing habitat nearby to which they could go.

Results

The food of the Mallard ducklings

Brood observations showed that almost all of the mortality occurred within the first twelve days of life, so for the purposes of this analysis the results are presented so that the food in the 0–12-day-old birds can be compared with that in the ducklings more than twelve days old. The results show that in each year's sample the 0–12-day-old ducklings had eaten more animal food items than those more than 12 days old (Table 4).

The number of food items, each food expressed as a percentage of the total, and the percentage occurrence of each food in the pooled sample are shown in Table 5.

Animal foods were found in 88% of the class Ia plus Ib sample (69 ducklings) and 60·6% of the items eaten were of animal origin, largely aquatic invertebrates. By comparison only 5·1% of the items found in the 30 ducklings which were between 12 and 45 days old were invertebrates, occurring in 53% of the sample. Diptera, mainly

Table 4. The foods of the Mallard ducklings collected in 1972, 1973 and 1974.

			Animal foods			Plant foods		
Year	Sample size	Age class	Number of items	%	% Occurrence	Number of items	%	% Occurrence
1972	12	Ia + Ib	133	46·7	92·0	152	53·3	75·0
	19	Ic – III	91	1·9	26·0	4682	98·1	84·0
1973	50	Ia + Ib	1979	52·6	86·0	1782	47·4	94·0
	5	Ic – IIb	75	6·0	100·0	1168	94·0	100·0
1974	5	Ia	871	98·9	100·0	10	1·1	40·0
	5	Ic – IIa	29	67·5	100·0	38	32·5	100·0

Chironomid adults, larvae and pupae were the main insect food in both groups, while adult Coleoptera were the most frequently found insect food, though they made up only a small percentage of the items. Aquatic molluscs, were also relatively frequent.

Eight (12%) of the ducklings in the younger age group, collected in May 1973, had eaten between 21 and 217 fish eggs, making these a relatively important but perhaps unusual food. Similarly 12·9% of the items eaten were the ephippia of the water flea *Daphnia* sp. but these were all found in one specimen. The proportion of plant food items, especially seeds, was much greater in the older ducklings than it was in the younger ones. By far the most important items were seeds of grasses occurring in almost half of the older sample.

In 1972 the main invertebrate foods of the

Table 5. The food of the Mallard ducklings. (Pooled sample.)

Food items	Classes Ia + Ib (69) Number of items	%	% Occurence	Classes Ic — III (30) Number of items	%	% Occurrence
Animal foods	3003	60·6	88	317	5·1	53
Diptera (adult)	193	3·9	23	47	0·7	27
Diptera (larvae)	201	4·0	19	49	0·8	13
Diptera (pupae)	562	11·3	15			
Coleoptera (adult)	252	5·1	62	43	0·7	33
Hemiptera (Heteroptera)	47	0·9	26	24	0·4	20
Ephemeroptera (larvae)	15	0·3	7	61	1·0	23
Trichoptera (larvae)	1	tr.	1	17	0·3	10
Hymenoptera (Formicoidea)	11	0·2	6	2	tr.	3
Zygoptera (adult)	1	tr.	1	4	tr.	7
Thysanoptera	1	tr.	1			
Collembola	14	0·3	1			
Arachnida	2	tr.	3			
Cladocera	640	12·9	1			
Other crustacea	2	tr.	3	4	tr.	3
Mollusca	126	2·5	29	57	0·9	20
Fish eggs	933	18·8	12			
Plant foods (seeds)	1955	39·4	87	5901	94·9	90
Rumex sp.	458	9·2	39	15	0·2	13
Potamogeton spp.	113	2·3	17	9	0·1	7
Eleocharis palustris	3	tr.	1	6	0·1	3
Grasses	434	8·7	31	4596	73·9	47
Cereal Grain				15	0·2	3
Polygonum spp.	45	0·9	19	73	1·2	33
Ranunculus spp.	58	1·2	4	1021	16·4	23
Compositae	89	1·8	3			
Galium aparine	3	tr.	3			
Juncus sp.	45	0·9	3			
Chenopodium album	7	0·1	3	9	0·1	3
Carex sp.	90	1·8	4			
Trifolium spp.	3	tr.	3			
Alnus glutinosa	3	tr.	1			
Zannichellia palustris	1	tr.	1	147	2·4	13
Rorippa amphibia	423	8·5	6			
Alisma plantago-aquatica	2	tr.	1			
Sparganium erectum	6	0·1	3			
Vegetative material			48			20
Unidentified remains	173	3·5	10	10	0·1	3

Note: Small quantities of vegetative material occurred in several ducklings. The air-filled tubercles from the sepals surrounding the seeds of the dock were the most frequent—35% occurrence, plus the following; *Potamogeton* spp. stem and leaf 3·9%, grass stem and leaf 3%, *Callitriche* sp. 2%, *Equisetum* sp. 1%, *Cyanophyte* 1% and *Elodea canadensis* 1%. In addition, fibrous plant material, often woody in nature was found in small quantities in 21% of the ducklings, in particular in three broods of 7 (Ia), 3 (Ib) and 4 (Ib) collected in the reserve in May 1973.

0–12 day old group were adult Diptera and Coleoptera, while in the older birds the small quantity of animal foods were sub-aquatic Hemiptera, Trichoptera larvae and Mollusca. A similar pattern was seen in 1974, adult Diptera and Coleoptera again being important in the young ducklings and sub-aquatic mayfly larvae being the most important invertebrate food in the older group. The pattern in 1973 is confused by the large number of fish eggs and *Daphnia ephippia* eaten by some of the younger group.

Insect emergence

The mean catch of each of the four insect traps used in 1975 is shown in Figure 2a as number per square metre. Three orders of insects were caught during the period of the survey, these were Ephemeroptera, Trichoptera and Diptera. Ephemeroptera were found in very small numbers throughout the period of operation of the traps, the main species being *Caenis moesta.*

Trichoptera were present in low numbers after early June. The most frequent species was *Mystacides longicornis*, present from 10th June onwards, and *Allotrichia pallicornis* was present in large numbers in trap 3 towards the end of June and formed an important part of the biomass emerging at this time.

Of the Diptera, members of three families only were captured, the most numerous being the Chironomidae which made up 98·0% of the catch. Some Ceratopogonidae were caught, the dominant species being *Probezzia venusta* and were all caught in trap 4. The other Diptera family was the Culicidae, represented by a few individuals of *Chaoborus flavicans.*

Over the period of the survey the emergence of most of the chironomids was predominantly from shallow water during June. Removal of the catch from four emergence traps every three hours for thirty-six hours on the 6th and 7th August showed that the peak emergence for the chironomids and most other insects, except ceratopogonids, occurred around dusk.

The insect survey of 1976 was designed to monitor the emergence of insects from different parts of the reserve over the whole of the duckling rearing season from 6th May to 20th August. No effort was made to identify the catch to species as it was assumed that the species composition of the catch would be similar to that found in 1975. The results are described separately for the four floating emergence traps, the three littoral emergence traps and the sweep netting of the waterside vegetation.

The peak emergence of insects into the floating traps was in the first two weeks of

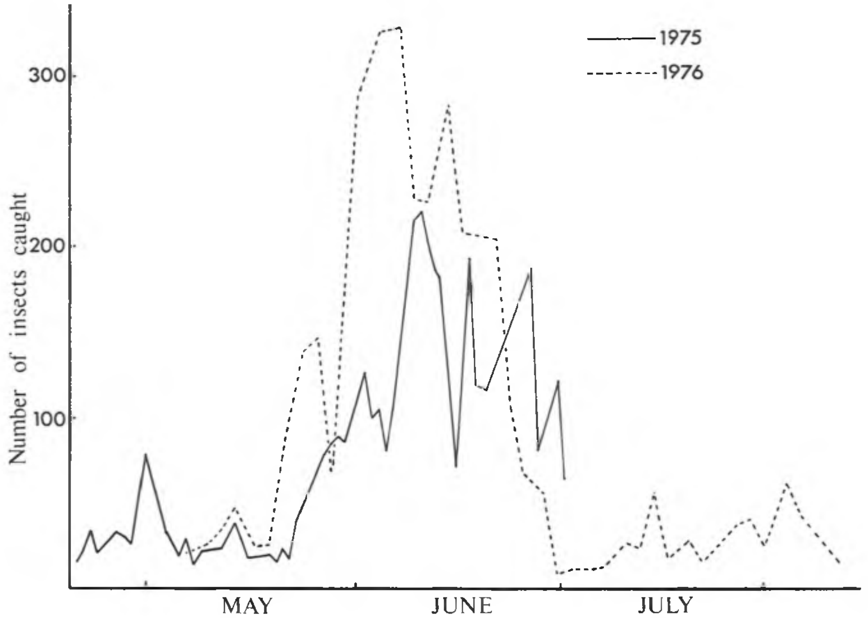

Figure 2a. The emergence of insects from the waters of the wildfowl reserve. (Mean catch per trap as number per square metre.)

June, and was at a very low level both before June and after July. The catches consisted mainly of chironomids (86·0% of the catch) with a few Culicidae and Ephemeroptera. Figure 2a shows the mean catch of each of traps 1–4 as number per square metre. The maximum number per unit area caught in these four traps was greater than that caught by the Mundie emergence traps in 1975, and this is probably due to the greater efficiency of the method of emptying the box traps.

The three littoral emergence traps showed similar trends in their catch (Figure 2b). The total number of insects caught was low until the last week in May, when it increased sharply, reaching a peak in the third week in June, after which the numbers caught fell rapidly to the pre-June level. Trap 5, over Bur-reed, had a peak catch in the last week of May and the first week of June, due mainly to the emergence of large numbers of ceratopogonids. The catch of trap 6, over Reed-grass reached a peak in mid June, again mainly of ceratopogonids. Trap 7, over Great Pond Sedge, produced peak catches in the last two weeks of June, also mainly of ceratopogonids but including many aphids. The mean catch of the littoral traps is shown as number per square metre in Figure 2b. The rapid fall in the catch of these traps in late June was due mainly to the fact that at this time the water level began to fall, exposing the base of the emergent reeds to the dying effect of the air. The soil became

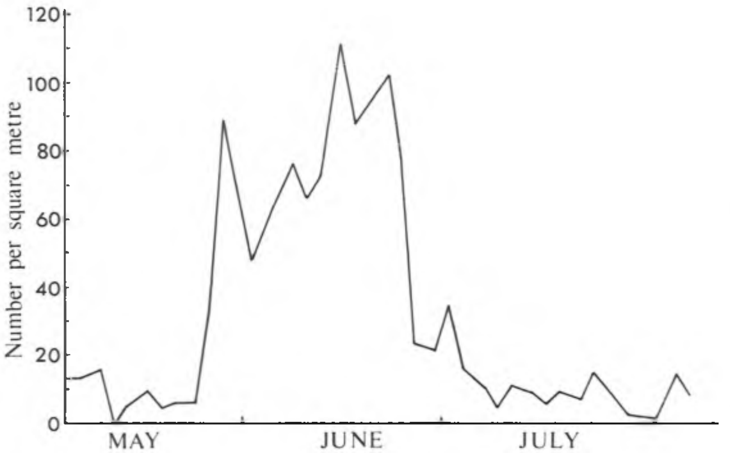

Figure 2b. The emergence of insects from the marginal vegetation in the wildfowl reserve, 1976. (Number per square metre.)

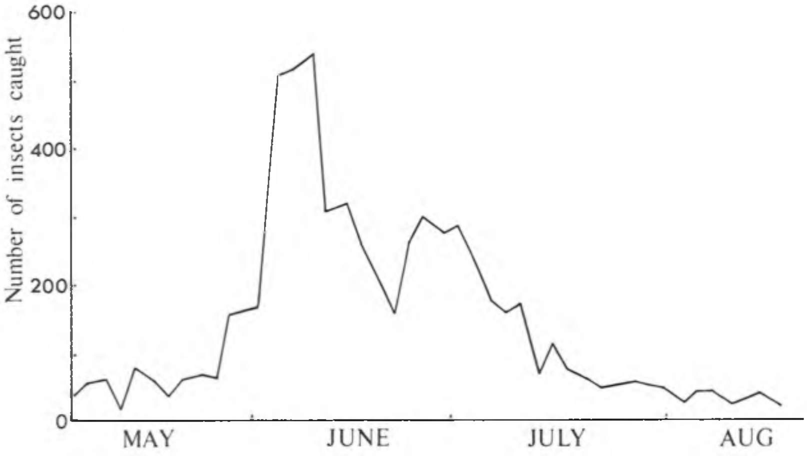

Figure 2c. The number of insects caught in the sweep netting of three 10 metre strips of waterside vegetation in the wildfowl reserve, 1976.

baked hard and dry and conditions were totally unsuitable for the aquatic invertebrates usually associated with these plants.

The numbers of insects caught in the sweep netting of the waterside vegetation (Figure 2c) increased rapidly to a maximum in the first week of June, after which the numbers declined gradually. The catch in this case was also mainly of chironomids. although there was an eruption of a chrysomelid beetle, *Gastrophysa viridula* on the nettle/thistle transect. Larvae were present in large number from 28th May to 16th June and adults from the 23rd June to the 9th July. At these times this species formed the major part of the catch and the numbers were estimated to the nearest 50.

The Mallard brood observations

Estimates of duckling mortality, by recording the decrease in brood size with increasing age, fail to take into account cases where a whole brood is lost. The brood sighting records suggest that this is a frequent occurrence at Great Linford. When brood sightings for 1974, 1975 and 1976 are pooled it is seen that while 61 records of class Ia (0–6 day old) broods were made, only 21 class Ib (7–12 day old) broods were observed, and 27 sightings were made of broods that were between class Ic (13 days old) and fledging. When repeat sightings are eliminated from the 1976 records it is seen that 25 different class Ia broods were recorded but only 10 different broods were seen that had graduated to class Ib, indicating that at least 60% of the class Ia (0–6 day old) broods were lost completely. Nine broods had survived until between 13 and 35 days old, of which at least 5 were known to have fledged.

The mean clutch size over the three years was $8 \cdot 3 \pm 0 \cdot 2$ and the mean size of class Ia broods was $6 \cdot 7 \pm 0 \cdot 4$, of Ib broods $4 \cdot 5 \pm 0 \cdot 5$, above Ic $3 \cdot 8 \pm 0 \cdot 3$ and at fledging $3 \cdot 3 \pm 0 \cdot 5$. Assuming a 95% hatch, these figures show that most of the reduction of brood size, i.e. the mortality within the average brood, also occurs between hatching and the 7th to 12th day of life, with the greatest losses in the first week; $43\% \pm 7 \cdot 5\%$ of ducklings were lost between hatching and class Ib. There was little mortality within the broods once they had survived for at least 13 days. Newton & Campbell (1975) showed that the average clutch size for the Mallard is larger early in the season, and so the duckling mortality among the earlier hatched broods may be greater than this overall estimate, while mortality among the later hatched broods may be correspondingly lower.

From these figures it appears that on average only 40% of broods produced survive beyond the first week after hatching. From the recorded decrease in mean brood size from hatching to the end of the first week of life, only 57% of the individuals in each brood survive beyond the first week. The survival rate of all the ducklings hatched in the study area is therefore at best 57% of 40%, i.e. 22·8% survival beyond the first week after hatching and there is undoubtedly some mortality after the first week. If 22·8% of the average hatch of 7·9 survive, the production would be 1·79 juveniles per pair of adults. From the differences in the spring and autumn counts of the Mallard population at Great Linford the production was estimated at 1·6 per pair in 1975 and 1·3 per pair in 1976. Boyd (1962) considered that 2·3 per pair was usual for this species in normal habitats.

The insect survey and temperature records indicated that conditions for Mallard ducklings were more suitable after 1st June in 1975 and 1976 so it was considered desirable to compare pre- and post-1st June mortality rates. When brood sightings for each year were separated into those broods hatched before 1st June and those hatched after, the frequency of sighting of broods of different ages in 1975 and 1976 suggested that total brood losses in the first twelve days of life were greater among the broods which hatched before 1st June (Table 6). When the two year's results are considered together it is seen that 36 sightings were made of

Table 6. The number of sightings of two age classes of Mallard brood in 1975 and 1976.

	1975		1976	
Age of broods	Hatched Pre-1st June	Hatched Post-1st June	Hatched Pre-1st June	Hatched Post-1st June
0–12 days (Ia + Ib)	11	8	25	17
13–50 days (Ic — Fledged)	5	8	5	11

0–12-day-old broods which had hatched before 1st June but only 10 sightings of these broods which had survived for 13 days or more and 25 sightings of 0–12 day old broods hatched after 1st June of which 19 sightings were made once they were more than 13 days old (these differences are significant, $\chi^2 = 3{\cdot}8$, $P = <0{\cdot}05$).

It has been shown experimentally that Mallard ducklings can grow very well on a diet of invertebrates alone. A feeding experiment carried out in June 1976 showed that game farm Mallard ducklings kept under paraffin heated brooders for 14 days, and fed *ad lib*, grew better on a diet composed solely of blowfly larvae, 51·8% dry weight protein, than ducklings fed on chick starter crumbs, 21% dry weight protein, and almost as well as ducklings fed on turkey starter crumbs at 26% by dry weight protein. Ducklings fed *ad lib* on a wholly plant diet, barley meal—13·5% protein, showed a very small weight gain over the 14 day period. The live weight gain per gram dry weight of food eaten was greatest in the invertebrate fed group. Further feeding trials are planned to investigate the value of more realistic seed diets and to determine the minimum proportion of invertebrate foods necessary in the diet to allow satisfactory growth and plumage development of young Mallard ducklings.

Discussion

The food requirements of the ducklings of some of the more common European species of ducks are incompletely known. Most of the studies have been carried out in North America. In all cases workers report that the downy ducklings readily eat invertebrate animals and Collias & Collias (1963) report that 'the distribution of broods of ducklings is roughly correlated with the abundance of invertebrates that apparently comprise their main food in the first week after hatching'.

The inclusion of material from the gizzard in the food analysis could have overemphasized the importance of the harder seeds as food items, although a low power microscope was used to examine the material for the harder parts of invertebrates in order to minimize this bias. Despite the possibility of such a bias it was found that the downy ducklings less than 12 days old ate a significantly greater proportion of animal food items than ducklings more than 12 days old in each of 3 years. The proportion of animal food, largely invertebrate, eaten by the class Ia and Ib ducklings was much less than reported by Bartonek (1972) and in the main North American study, that of Chura (1961). He also used gullet/gizzard contents and found that class Ia Mallard in natural wetland habitat in Utah consumed animal food exclusively, class Ib consumed 90% animal food, class Ic 75% animal food, class IIa 50% animal food and 50% plant food (mainly seeds), class IIb 70% plants and class IIc 92% plants. He pointed out that the majority of invertebrates consumed by the class Ia Mallard were Tendipedidae adults (Chironomidae) and these were also the most important invertebrates found in the younger groups of ducklings from Great Linford.

Chura also noted that there was a marked switch from aerial to aquatic invertebrate foods between classes Ic and IIa. This was true to a certain extent in this investigation, but it occurred much earlier, along with the change to a predominantly seed diet.

Bengtson (1975), in the analysis of 16 small to slightly more than half-grown Mallard from Lake Mývatn, found that 80% by wet weight of the food material was plant foods (seeds) and of the 20% animal foods, dipteran adults were the most important, adult chironomids being found in nearly every duckling. Although most of the wet weight of the food was seeds, Bengtson stated that most of the oesophagus samples contained considerable numbers of adult insects, chiefly chironomids and simuliids, and he therefore considers insect food to be an important requirement.

If the proportion of animal foods found in the ducklings examined in this study and by Chura (1961) were expressed as a percentage of the total weight of foods found, the proportion of animal foods would appear to be less, due to the relatively larger size and greater weight of the individual plant food items which were mainly seeds. The differences between the results of the different investigations would, however, remain the same. The proportion of animal food found in the very young ducklings taken at Great Linford was not nearly as great as that found in the ducklings examined by Chura. The change to a predominantly seed diet also occurred much earlier, well before class IIa, in the duckling sample collected from the gravel pits.

Little mention is made by other workers of the consumption of vegetable material except for the occurrence of *Polygonum* spikes and bulbils and the blue-green alga *Nostoc* (Bengtson 1975) and *Potamogeton pecinatus* tubers (Chura 1961). The fibrous plant material and dock sepal tubercles found in some of the Great Linford ducklings was probably of minimal food value, but the small amounts of greenstuff found in a few ducklings may have been of some nutritional value. Kear (1965) states that inedible items such as eggshell, down and nest material are invariably swallowed as the first 'food' of Mallard ducklings and perhaps the woody fibres found in some young birds in this study is an example of this. It is thought that these inedible items are swallowed to initiate peristalsis and stimulate proper feeding activity.

It is postulated that the relatively low consumption of invertebrate foods by ducklings hatched at Great Linford reflects a low availability of such foods, especially of the aerial forms, in the gravel pit study area, which in turn is largely responsible for the high rate of mortality observed among Mallard in the first week of life. The reason why the very young ducklings are so dependant on a good supply of freely available invertebrate foods is that for a fast growing animal, the limiting factor in any diet is normally the level and digestibility of its protein content.

Sturkie (1954) showed that temperature control in a wide range of birds does not become fully effective until complete development of juvenile plumage and resistance to chilling increases as the plumage develops. Cross (1966) demonstrated experimentally that the growth of Partridge *Perdix perdix* chicks was fastest on a high protein insect diet and that the time taken to resist chilling was probably related to body weight.

It follows that the rate of growth and therefore of plumage development would be more rapid in a duckling feeding on a high protein insect diet than it would in a duckling feeding on a diet composed mainly of seeds such as grass seeds which have an average protein content of 12·2% (Titus 1961). The duckling on the seed diet would therefore be vulnerable to the effects of chilling for a longer period than the insect fed duckling and would therefore stand a reduced chance of survival in the wild.

Further evidence that ducklings need invertebrate foods comes from Moyle (1961) who states that laying hens, ducklings and moulting adults can not obtain their necessary protein and specific amino acid requirements from an entirely plant diet, Sugden (1973), 'there is considerable variation in the amino acid composition of the different foods, and none of the plant foods found meets all of the requirements of waterfowl. Of the 13 foods identified, chironomid larvae, corixids and gammarids would appear to provide the most complete range of amino acids as based on chick requirements'.

Analysis of the protein content of various insect groups by Cross showed that there was little variation between the groups investigated, the average protein content being between 40 and 58% by dry weight. A sample of mixed invertebrates similar to those eaten by the downy ducklings, mainly adult chironomids plus some aquatic invertebrates, aphids and beetles, was collected from the study area and on analysis was found to be 44·8% by dry weight protein. The minimum daily requirement of protein by wild Mallard ducklings is not known although Holm & Scott (1954) found that a level of 19% protein in the diet of wild ducklings of several species, including Mallard, was sufficient. This, however was under artificial conditions where food was provided *ad lib.* They stated that wild waterfowl are able to balance their diets with widely different foods, the primary consideration being the availability of sufficient protein, carbohydrate, fats, minerals and vitamins, regardless of the source. A wild duckling may be able to adjust its intake of low protein food to obtain its requirements for growth where foods are unlimited and where a great deal of time can be spent feeding, but where foods are not freely available and under the adverse weather conditions so frequent in the wild, a high protein insect diet may become essential.

Cross (1966) estimated that the minimum daily intake of 'average' insect food for a 9-day-old Partridge chick weighing 18 gm would be 1·95 gm dry weight. A Mallard duckling on hatching usually weighs 34 gm (Kear 1970) and so assuming similar needs its requirement of insect food would be nearly twice this value per day. This represents a considerable quantity of insects, approximately 1,050 adults of a large species of chironomid, requiring an abundant and freely available supply of insects in the habitat. Otherwise more time is spent on searching for insects or alternatively, more easily 'captured' seeds are eaten. Even a short spell of inclement weather would be sufficient to prevent the duckling obtaining its daily protein needs. This would result in retarded growth and increased susceptibility to chilling. Weakness due to lack of sufficient insect food would also mean increased susceptibility to separation from the adult female and to attacks by predators. There is also evidence (Fabricius 1947) that insect food is essential for the maintenance of waterproof condition of the downy plumage of Tufted ducklings, and this may be true of all ducklings. So the weakness caused by the lack of insect food is rapidly followed by waterlogging, chilling and death.

The monitoring of the emergence of adult insects from the waters of the reserve showed that the aerial insect population so essential for the very young ducklings was dominated by one group, the Chironomidae, and that emerging insects were present in relatively large numbers for a limited period only, during the first two weeks of June. So ducklings hatching in the study area have a relatively abundant insect food supply for this limited period only. The observations on duckling mortality show that most deaths occur in the first few days after hatching, and early in the season, before 1st June. It is possible that this may be due in part to the fact that weather conditions are generally better after 1st June, allowing more time for feeding.

The productivity of the new gravel pit habitat in terms of emerging insects is low because of the ecologically immature, oligotrophic status of the artificially made aquatic environment (Birch 1971). Aquatic macrophytes are not abundant, and the sediments, if any, of the new lakes have a relatively poor nutrient status as there has been insufficient time for the accumulation of the organic material so necessary for the production of aquatic insect larvae. Hence the lack of insect diversity and low productivity. The Chironomidae appear to be able to adapt to these conditions most successfully although their rate of production is also thought to be limited by the conditions.

Two series of Ekman grab samples taken at trap sites 1 to 4 (one sample per site) on 15th April and 30th April 1975 showed that the mean density of chironomid larvae at these sites on those dates was $422/m^2$ and $822/m^2$ respectively. In comparison, the average density of four dominant species of chironomids at Loch Leven over the period March 1971 to March 1972 was $11{,}223/m^2$, and in May 1971 the density of final instar larvae of the same four species was approximately $3{,}400/m^2$ (Charles *et al.* 1972).

In the sediments of the more eutrophic waters the larval density can be extremely high. Mundie (1957) found that the standing crop of chironomid larvae in Kempton Park East reservoir, London, in March 1952 was $34{,}000/m^2$ at 6·8 metres depth, and $46{,}000/m^2$ in the littoral at 1·0 metre. Mundie's annual catch of the adults of the six common species was $13{,}000/m^2$, all emerging between April and October. At Great Linford the total catch of all species of chironomid from May to August was $3{,}239/m^2$ in 1975 and $2{,}986/m^2$ in 1976. Mundie found 60 species of chironomid in the reservoir, while only 32 species were identified at Great Linford.

If the duckling mortality in the gravel pit is due mainly to the lack of insect foods, which is due in turn to the poor quality of the new wetland habitat, then one would expect the mortality to be greater than that observed in natural, more productive wetlands and this does indeed appear to be the case. Estimates of duckling mortality reported in the literature are generally lower than that found at Great Linford (at least 77%). Bengtson (1972) estimates that from a similar clutch size (8·5), 9·3% failed to hatch and 53% of the dabbling ducklings at Lake Myvatn survived to full grown. The studies dealing with waterfowl brood success in North America and Europe also report that the greatest losses are among the newly hatched ducklings (Munro 1943; Earl 1950; Eygenraam 1957) but that mortality is relatively low at 20 to 50% with an average of 30% (Girard 1941; Earl 1950; Harris 1954; Miller & Collins 1954; Steel *et al.* 1956; Keith 1961). Boyd & Campbell (1966) estimated that out of 1,640 Mallard leaving nests at Loch Leven, 1,100 were fledged, i.e. 67% survival. This estimate may be slightly exaggerated as it does not take into account complete brood losses. Using similar brood census methods, Hildén (1964) found that duckling mortality on poor quality habitat in the island group of Valassaaret, Gulf of Bothnia was concentrated in the first three weeks after hatching, after which it fell significantly. His figures are very similar to those found in this study. Hildén also reported that complete brood losses early in the season were high, in spite of the early start to breeding he never saw a fully fledged Mallard before the beginning of August. At Great Linford in 1976 the first newly hatched brood was seen on 28th April and the first fledged duckling was seen on the 3rd August. In comparison, Mallard breeding on better habitat on inland Finnish lakes at Central Häme had a much better survival rate than that at Valassaaret (Linkola 1962).

The major cause of losses proposed by other workers is bad weather, especially air temperatures below 2°C, precipitation and high winds (Bengtson 1972); Boyd and

Campbell (1966) state that bad weather probably killed more ducklings than did predators at Lock Leven. Predation is not generally considered to be important as a cause of duckling losses, although Solman (1945) suggested that pike could remove up to 10% of the annual production of ducklings in Saskatchewan river deltas. The size of the pike population of the study area is not known, but the number of ducklings lost to this predator is assumed to be very small. All other potential predators are controlled within the study area.

Newton & Campbell (1975) state that crowding of broods at Loch Leven causes intraspecific aggression, resulting in many duckling deaths. This overcrowding of broods has not been observed at Great Linford and such aggression is not thought to be important as a cause of duckling losses.

While unfavourable immediate weather conditions are probably the proximate cause of death in most cases, it is reasonable to assume that a well nourished, rapidly growing duckling in a highly productive, insect rich wetland can withstand unfavourable conditions much better than one which is only just managing to maintain itself on a poor diet. The results of the feeding trials mentioned earlier showed that ducklings can not grow satisfactorily on a diet composed solely of seeds, whilst they can on an invertebrate diet.

The results presented in this paper suggest that the primary cause of the high mortality of Mallard ducklings at Great Linford is the low productivity of suitable insect foods.

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Summary

This paper describes the food found in Mallard *Anas platyrhynchos* ducklings in the gravel pit study area at Great Linford, Buckinghamshire, and relates the unusually high duckling mortality, estimated to be at least 77%, to the relatively low consumption of insect foods by the downy ducklings. The emergence of insects in the breeding reserve was monitored and the duckling mortality was observed to be greatest before the peak of insect emergence in June. It is suggested that the low comsumption of essential invertebrate foods is a result of the reduced availability of such foods because of the low productivity of the man made, ecologically immature newly flooded gravel pit habitat.

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