Effects of increasing larval chironomid densities on the underwater feeding success of downy Tufted ducklings *Aythya fuligula*

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This study relates the underwater feeding success of downy Tufted ducklings (aged 14-25 days) to differing levels of food (chironomid larvae) availability. Feeding success (chironomids caught per dive) increased from an average of about one at a prey density of 2000/m² to six at 8000/m² and around 12 at 16,000/m². Ducklings also increased their mean dive duration and total foraging effort with increasing prey density. Over the range of food densities used in the present experiments, ducklings showed no sign of becoming limited by time in their ability to catch more prey per dive at high prey densities. This study shows that despite dives only lasting around 3 seconds, ducklings still have time available to catch and 'handle' up to 14 chironomid larvae per dive. At the highest food density tested ducklings could, by selecting the largest available larvae, fulfil their daily food requirement in 36 minutes of underwater foraging. This period is greatly affected by prey size and prey density. More experiments are needed to establish the food density at which feeding success reaches a plateau. These results are discussed in relation to the literature available for other wildfowl and wading bird species.

There has been considerable recent interest in the role of food availability as a factor influencing duckling survival in the wild. Several authors have suggested that a low availability of aquatic invertebrates (particularly insects) leads to poor duckling survival; this argument has been used for the following species: Mallard *Anas platyrhynchos*, Street (1977), Pehrsson (1984), Hill *et al.* (1987), Giles *et al.* (in prep); Tufted Duck *Aythya fuligula*, Hill & Ellis (1984), Giles *et al.* (in prep); Black Duck *Anas rubripes*, Hunter *et al.* (1984, 1986); Goldeneye *Bucephala clangula*, Erikson (1978); Long-tailed Duck *Clangula hymenalis*, Pehrsson (1974) and Common Scoter *Melanitta nigra*, Partridge (1989). A causal link between invertebrate availability and duckling survival has, however, proved difficult to demonstrate.

Laboratory experiments provide some supporting information, allowing the direct manipulation of the quality and quantity of the food supply whilst following some measure of duckling feeding success. Street (1978) used young Mallard ducklings to demonstrate that access to a protein-rich (*Calliphora vulgaris larvae*) food supply led to a rapid duckling growth rate. At least 50% dry weight of insect larvae needed to be added to a mixed seed diet before young Mallard ducklings showed a weight gain. Giles (1989) has shown that captive downy Tufted ducklings approximately doubled their foraging success (on chironomid larvae) when the food density on the bed of an experimental tank was doubled. The larval chironomid densities used (2000 and 4000 per square metre) were representative of those found naturally in the gravel pit lakes at the ARC Wildfowl Centre study site. Natural lakes, however, often have much higher densities of chironomid larvae than these, e.g. Loch Leven (where Tufted Ducks are known to eat chironomid larvae, Laughlin (1973)) has a peak abundance of more than 54,000 larvae per square metre in July (Maitland & Hudspith 1973). The present paper combines the results of further laboratory experiments on Tufted ducklings, which were allowed to forage over a gravel substrate containing larval chironomid densities of 2000-16,000 per m², with the results from Giles (1989), to examine the relationship between food supply and feeding success in diving ducklings. The findings are then related to the likely response of diving ducklings under natural conditions to increased levels of available food.

Methods

Two clutches of Tufted Duck eggs were hatched in 1989 to provide ducklings for experiments on

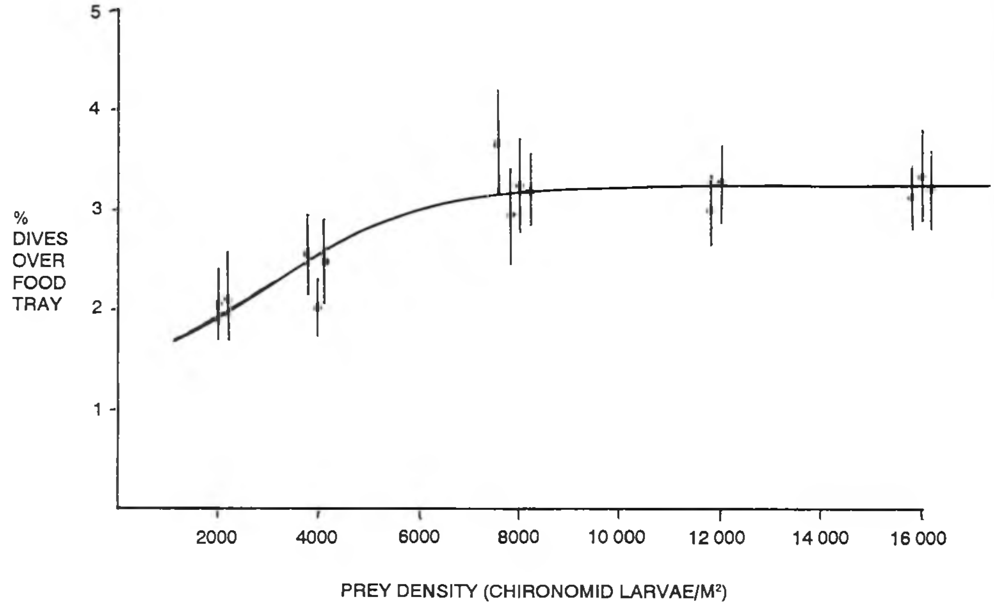

Figure 1. Mean dive durations (± 2 S.E.) for the two broods of Tufted ducklings used in 1989 experiments.

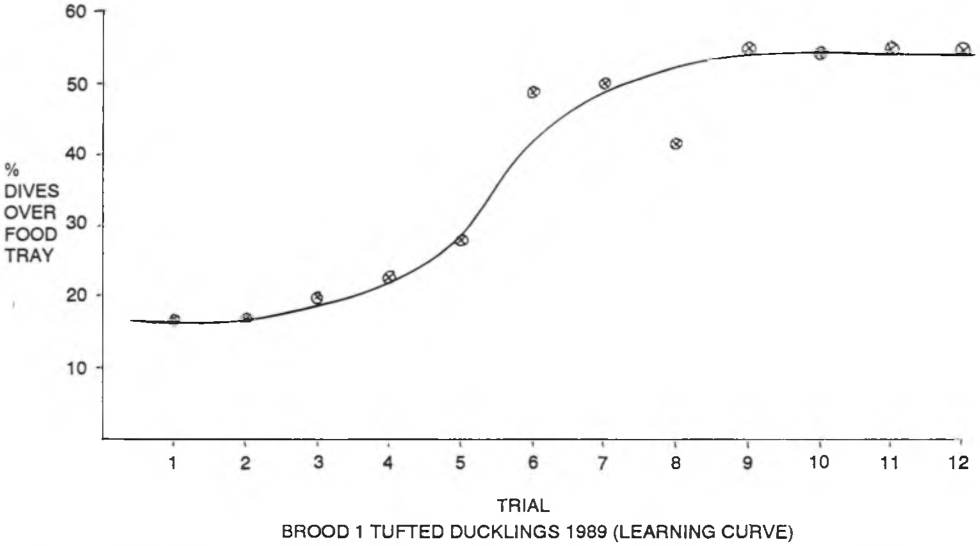

Figure 2. The proportion of dives per trial made over the food patch by the first brood of Tufted ducklings.

their feeding behaviour. One was picked up from the wild (under NCC licence) in mid-June and the other was obtained from captive birds (A. Zwetsloot, Sandy, Bedfordshire). The ducklings were reared in large fibreglass rearing pens with access to water for swimming and diving at all times. The water was covered with a layer of duckweed *Lemna minor* which also contained an abundance of aquatic invertebrates including *Asellus, Gammarus, Ephemeroptera* nymphs and (introduced) chironomid larvae, all of which the ducklings ate. Ducklings were also fed *ad lib.* on turkey starter crumbs (26% protein) and *Calliphora vulgaris* larvae. An infrared brooder lamp was available to the birds at all times. The first brood of eight ducklings was used for experiments at an age of 15-18 days and the second brood, also of eight, at an age of 24-25 days. (Data from Giles (1989) was obtained using birds of 14-18 days age.) The experimental design was identical to that used in Giles (1989), i.e. a large (1.5 m x 1.0 m x 1.0 m) glass aquarium with a gravel bed was used to allow ducklings to dive over a food patch which they rapidly learnt to locate and exploit. The water depth in all experiments was 75 cm. The food patch consisted of a fine-meshed wire tray (800 cm^2 in 1989) filled with gravel where *Chironomus plumosus* larvae were allowed to burrow prior to a feeding trial. Chironomid larvae were purchased from an angling supplies shop where they are sold for fishing bait (as "bloodworm"). Each experimental run consisted of a period of approximately 20 minutes with the following recorded: total number of dives outside food tray, total number of dives over food tray and (for all but one trial) the duration of each dive over the food tray. Birds needed to rest and preen after 20 minutes of repeated diving. Before the beginning of an experimental run a known number of chironomid larvae was allowed to burrow until all were out of sight. After the ducklings had fed the tray was retrieved, the gravel sieved and the total number of surviving chironomid larvae counted. Thus the number (and %) of chironomids eaten during each test, the average number of chironomids eaten per dive over the food tray and the proportion of the total dives which were made on to the food tray were obtained. In 1989 densities equivalent to 2000, 4000, 12,000, and 16,000 per m^2 were used, with additional data for 2000 and 4000 from the 1988 trials included.

Results

Duckling broods which were new to the experimental tank explored the water surface for food before starting to dive. Individuals dived over all areas of the tank bed, with bursts of diving activity being interspersed with rest periods. Whilst underwater, ducklings searched for food both visually and by very actively probing the gravel with the tip of the bill. The prey was captured by rapidly opening and closing the mandibles below the gravel surface; food was apparently detected by "touch".

The mean dive durations (± 2 S.E.) for the two broods of Tufted ducklings used in 1989 experiments are given in Figure 1. The first brood (aged 14-18 days) provided all the data points except those trials run at a prey density equivalent to 12,000 chironomid larvae per m^2 which were recorded for the second brood (at age 24-25 days). Whilst dive time is known to increase with age (5-50 days) in Tufted ducklings (Hill & Ellis 1984) there is little increase between the ages 14-25 days; the age range of the ducklings used for the present study. Age is unlikely, therefore, to have an important effect upon the results from the present study. Mean dive duration increased from a value of *c.*2 seconds at prey densities of 2000 per m^2 to just over 3 seconds for densities of in excess of 8000 per m^2 (Fig. 1). In 1988 the mean dive duration of similarly aged Tufted ducklings feeding over a food density of 2000 chironomid larvae per m^2 was also *c.*2 seconds (Giles 1989). An increase in dive duration of *c.*1 second provides the ducklings with 50% more foraging time underwater per dive. The proportion of dives per trial made over the food patch by the first brood of ducklings with an increasing number of trials is given in Figure 2. The resulting curve (fitted by eye) is sigmoid, with a plateau level of >50% of all dives being directed at the food tray. During this series of trials food density increased so that the increasing proportion of dives over the tray could be due to a combination of both learning, and increased feeding effort over higher food densities. In earlier experiments Tufted ducklings foraging over a constant food density showed a steep learning curve, with the brood increasing the proportion of dives made over the feeding tray from 4% in the first trial to *c.*25% after ten trials (Giles 1989). The mean diving success (average number of chironomid larvae eaten per dive, pooling all available data) is given in Figure 3. As prey density increases diving success increases linearly. The regression equation describing this relationship is: Diving success (mean number of chironomids eaten per dive)

$$= -0.51 + 0.00087 \times P$$

Where P is prey density, expressed as numbers per square metre, at the start of each experiment.

Coefficient of determination = 0.96

This apparently close association between feeding success and initial prey density is however influenced by the fact that the data used were those for mean feeding success in a given trial; thus losing the actual variation in success in individual dives. This was inevitable because of the impossibility of recording how many larvae were captured by each duckling on each dive. The loss of the individual diving success data reduces the variance around the least-squares linear regression and increases the value of the correlation coefficient. Despite this short-

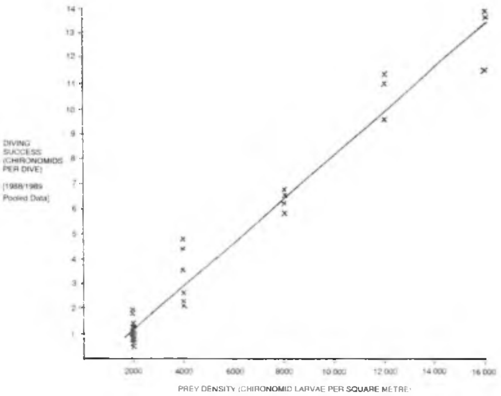

Figure 3. The mean diving success (average number of chironomid larvae eaten per dive) v. food density at the start of the experiment.

coming the underwater feeding success of downy Tufted ducklings appears to be closely related to food density at the start of each experiment.

The initial number of prey used in each 1989 trial, the number and percentage eaten, the number eaten per dive and proportion of initial prey number eaten per dive are given in Table 1. These data show, firstly that given an average dive duration of *c*.3 seconds it is surprising that ducklings caught and ate, on average, up to 14 larvae per dive at the highest prey density. Allowing 0.5 seconds to reach the tank bed and 0.5 seconds to return to the surface the birds were catching up to seven larvae per second whilst searching through the gravel for food items, giving a prey handling time of 0.14 seconds at the highest prey density tested (16,000 per m^2). This success rate dropped to *c*.3 per second at the lowest prey density (2000/m^2). Most trials lasted for 18-20 minutes by which time an average of 140 dives had been made of which *c*.60% were directed on to the food tray. The duckling broods depleted the food supply by 20-54% at lower food densities and by over 80% at higher densities. Despite the changing prey densities and changes in dive times the average proportion of available prey eaten per dive remained almost constant at *c*.1% (Table 1).

Discussion

The broods of Tufted ducklings observed during the present study had received no parental care and were feeding over a bare gravel substrate which had little or no food visible on the sediment surface, nevertheless they showed highly efficient foraging behaviour, in line with previous results (Giles 1989). The present study has indicated the importance of prey density under conditions where the feeding area and substrate composition have been held constant. The key restraints determining underwater foraging success include;

a) area of substrate covered in the (very short) time available
b) prey quality, density and distribution
c) capture efficiency and prey handling time.

I have not observed any instances of intraspecific aggression either within or between Tufted duckling broods which could reduce foraging efficiency under either natural or laboratory conditions.

Table 1. Feeding performance of 15-20 day old Tufted ducklings in 1989 experiments.

Prey at start of experiment *n*	Prey eaten during experiment *n*	% of initial number eaten in total	Prey eaten per dive *n*	Proportion of initial number eaten per dive
160	47	29	1.8	1.1
160	34	21	1.1	0.7
320	146	45.6	4.4	1.3
320	172	53.7	3.5	1.0
320	171	53.4	4.8	1.5
640	420	65.6	6.7	1.0
640	316	49.3	6.2	0.9
640	370	57.8	5.7	0.9
640	464	72.5	6.6	1.0
960	300	31.2	9.6	1.0
960	631	65.7	11	1.1
960	451	46.9	11.4	1.1
1280	916	71.5	11.5	0.8
1280	1072	83.7	13.9	1.0
1280	1082	84.5	13.8	1.0

Several species of diving duck have now been used for diving trials in captivity, e.g. Tufted Duck and Pochard *Aythya ferina* by Draulans (1987), Ruddy Duck *Oxyura jamaicensis* by Tome (1988, 1989), Lesser Scaup *Aythya affinis* and Canvasback *Aythya valisineria* by Tome & Wrubleski (1988). Most of this work has been directed toward initial descriptions of the observed underwater feeding behaviour, followed by experiments to test whether the exploitation of food patches by these ducks conformed to predictions from optimal foraging models. The present study has the simple, practical aim of establishing whether, under standardised laboratory conditions, downy Tufted ducklings find and eat larger numbers of burrowing chironomid larvae at increasing prey densities and, if so, what is the relationship between foraging success and prey density?

The recent research work at Great Linford has been directed towards increasing the availability of aquatic invertebrates as food for wildfowl; this has been accomplished primarily by the removal of fish (mainly bream *Abramis brama,* perch *Perca fluviatilis,* roach *Rutilus rutilus*, tench *Tinca tinca* and pike *Esox lucius).* After the removal of a total of seven tonnes of fish from *c.*18 ha of water invertebrate standing crops (including those of the chironomid larvae) increased substantially (Giles *et al.* in prep). This has created the potential for better survival of both Mallard and Tufted ducklings which, prior to fish removal, typically had a mortality rate of 80% in the first two weeks after hatching (Hill & Ellis 1984, Hill *et al.* 1988). Tufted Ducks now use the wildfowl sanctuary for brood rearing whereas in previous years they took newly hatched broods to rearing habitat outside this reserve area. Brood observations within the wildfowl sanctuary in the summer of 1989 indicate that Tufted duckling fledging success rose from the previous *c.*2 per brood to *c.*4 per brood; more data are needed however to check the validity of these preliminary findings (Traill-Stevenson & Giles 1990). The laboratory results reported in the present paper indicate that downy Tufted ducklings should benefit directly from increased macroinvertebrate standing crops by gaining a much higher food intake per dive. Potter & Learner (1974) give figures for the mean dry weights of 1st, 2nd, 3rd and 4th instar *Chironomus plumosus* larvae. In the present study most of the chironomid larvae used were fourth instar which weigh *c.*4.4 mg dry weight but some third instar larvae weighing *c.*0.23 mg dry weight were also present. These figures can be combined with Kear's (1970) estimate of the food consumption of 21-day-old Tufted ducklings of 44 g dry weight of food pellets per day to calculate the following comparisons. Assuming a similar nutritional content for growers pellets and chironomid larvae (both as dry weights); 44 g of pellets = 10,000 4th instar *C. plumosus* larvae or 191,304 3rd instar larvae. The ducklings in the present study caught, on average, up to 14 larvae per dive at a food density of 16,000 per m^2 thus needing 714 dives to catch 10,000 4th instar larvae. Each dive lasted, on average, 3 seconds in total, therefore, 2142 seconds or 35.7 minutes of underwater foraging time would be needed to fulfill the estimated daily food requirement. If the birds were restricted to 3rd instar larvae (weighting 0.23 mg) they would need to feed for 11.38 hours. A diet of 50% 4th instar and 50% 3rd instar larvae at the highest food density would impose a total daily feeding duration of 6 hours. At a food density of 8000 larvae per m^2 ducklings caught six larvae per dive and would need 1666 (3 second) dives, i.e. a total of 83 minutes underwater foraging time to catch their daily 10,000 larvae. Prey size clearly has a great potential to affect foraging efficiency in these birds. These approximate calculations serve to illustrate the importance to diving ducks of capturing large, nutritious prey items whenever possible to minimise the energy and time expended during foraging. The quantitative benefit derived in the wild will obviously be different from that reported in the present paper since in nature the substrate is of variable composition and a variety of prey taxa are available as food.

The need for rich feeding habitats by adult diving ducks is also demonstrated by the work on Ruddy Ducks by Tome & Wrubleski (1988) and Tome (1988, 1989). As in the present work with Tufted ducklings, adult Ruddy Ducks were found to a) stay on one food patch and deplete it severely before moving on to look for a new patch (Tome 1988) and b) revisit previously profitable patches more often than would be expected by chance (Tome 1989). Underwater search paths over food patches were longer in length and duration, had a lower velocity and were more sinuous than in areas devoid of food. Search path durations were also shorter in low density food patches than over higher density patches (Tome 1989). Adult Ruddy Ducks normally feed on benthic invertebrates (including chironomid larvae) by moving the bill through lateral arcs while rapidly opening and closing the mandibles (Tome & Wrubleski 1988). The food source used for the above experiments was, however, wheat grains since chironomid larvae were difficult to obtain in sufficient quantities to run the experiments.

In the present study it is clear that there must come a point at which dive duration, handling ability, satiation and prey depletion limit the increase in feeding success with prey density. This point of levelling of the curve was not reached in the present study even at prey densities of 16,000/m^2. This is, perhaps, not surprising since natural chironomid prey densities can reach at least four-five times this value (e.g. Maitland & Hudspith 1973). Running experiments at prey densities of *c*.50,000 chironomid larvae/m^2 becomes a daunting prospect when it is realised that the 1989 trials necessitated obtaining and counting a total of 14,528 chironomid larvae (10,560 to start the trials plus 3968 surviving larvae). The use of wet weights of larvae would, however, make such experiments feasible.

Field studies on shorebirds have investigated the relationships between feeding ecology and prey availability in the wild. Goss-Custard (1977a) studied the feeding ecology of wintering Redshank *Tringa totanus* at several sites in the south of England. He found that birds feeding on the amphipod crustacean *Corophium volutator* by probing the estuarine substrate ate *c*.30 per minute feeding at prey densities of 2000 *Corophium*/m^2. In the present study Tufted ducklings probing the substrate for chironomid larvae also ate 30 per minute feeding at a prey density of 2000/m^2. At higher prey densities (5000-6000/m^2), however, Redshank fed at reduced rate of *c*.25 per minute whilst, in the present study, Tufted ducklings ate 96 chironomid larvae/minute at 4000/m^2. Reference to Table 1 in the present study (percentage of prey eaten) shows that the overall proportion of the total prey taken by a brood of Tufted ducklings in a given trial tends to rise with prey density. This association is probably a mixture of learning the presence of the food source (Fig. 2) and an increased foraging effort with increasing prey density. The relative importance of learning and prey density effects can only be quantified from further laboratory experiments.

Phillips (in press) has recently shown that Pochard wintering at Great Linford select areas of relatively high larval chironomid densities (and biomass) to feed over, concentrating 77% of feeding dives in one small bay of a single lake.

It seems likely therefore that both diving ducklings and adult diving ducks can respond rapidly to changes in the benthic invertebrate food supply by concentrating their foraging over areas of the highest habitat quality. This behaviour is likely to have beneficial consequences both for duckling survival and the maintenance of body condition in wintering birds. Talent *et al.* (1982) have shown that Mallard nesting on seasonal ponds in North Dakota select brood rearing sites with relatively high densities of chironomid larvae (up to 5300/m^2) and Haland (1983) argues that competition between Mallard broods for invertebrates may regulate brood spacing. Pehrsson (1984) has emphasised the importance of abundant aquatic invertebrates for both pre-laying Mallard in spring when they need a high protein intake and for duckling diet in May and June. Danell & Sjoberg (1978) found that the hatching of Mallard, Teal *Anas crecca* and Pintail *Anas acuta* ducklings in Sweden was timed to coincide with peak adult chironomid availability. Abundant chironomid populations are, therefore, likely to benefit both diving and dabbling ducks throughout their lives and habitat management to increase aquatic invertebrate production should provide a method of maximising the value of lakes as waterfowl conservation areas (Giles *et al.* in prep).

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Young Tufted Duck diving for food. *Photograph by the author.*