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SIZE SELECTION IN DIVING TUFTED DUCKS *Aythya fuligula* EXPLAINED BY DIFFERENTIAL HANDLING OF SMALL AND LARGE MUSSELS *Dreissena polymorpha*

JOEP J. DE LEEUW[1] & MENNOBART R. VAN EERDEN[2]

ABSTRACT We studied prey size selection of Tufted Ducks feeding on freshwater mussels under semi-natural conditions. In experiments with non-diving birds, we found that Tufted Ducks use two techniques to handle mussels. Mussels less than 16 mm in length are strained from a waterflow generated in the bill (suction-feeding), while larger mussels are picked up and handled singly. Suction-feeding on small mussels proved to be more profitable. In the non-diving situation, the ducks preferentially took the smallest mussels on offer. It is suggested that smaller mussels incur lower costs of crushing mussel shells in the gizzard. Ducks diving for mussels preferred suction-feeding on all mussels up to about 16 mm in order to minimize the costs of diving. The selectivity for small mussels increased with diving depth (1 - 5 m), probably because ducks diving deeper spend more time at the bottom collecting small mussels, before a larger mussel is taken to the surface and ingested afterwards. We conclude that the two handling techniques we described for Tufted Duck open up an extensive feeding niche for benthic feeding diving ducks.

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INTRODUCTION

Birds feeding by diving must regularly interrupt feeding to return to the water surface to breathe. In most birds, dive times are short (i.e. less than one minute; Dewar 1924, Kooyman 1989) and consequently the decision of which prey to take will be focussed on collecting prey in very short feeding bouts. Recently, it has been shown that prey choice may be influenced by the period of time over which foraging decisions take place (see Lucas 1990, for review).

In this study we examine prey choices in a diving bird, the Tufted Duck *Aythya fuligula*. In the wintering areas in western Europe, Tufted Ducks mainly feed on Zebra-mussels *Dreissena polymorpha* (e.g. Bij de Vaate 1991). All mussels are swallowed whole and crushed in the muscular gizzard. Shell fragments and flesh pass together through the gastro-intestinal tract. Both in field studies (Pedroli 1981, Draulans 1982) and in captivity (Draulans 1982, 1984, 1987), it has been shown that Tufted Ducks select particular mussel sizes. Draulans studied size selection in relation to the profitability of the prey and found that Tufted Ducks selected smaller mussels than would be expected. His explanation was that the birds avoided the risk of taking mussels that were too large to be swallowed and hence unprofitable (Draulans 1984). In his experiments, however, the ducks did not have to dive for the mussels.

Tufted Ducks in the wild feed predominantly by diving at depths up to 5 m (Willi 1970, Nilsson 1972, Draulans & De Bont 1980). The aim of this paper is to study the impact of diving on prey size selection. Experiments were carried out with captive Tufted Ducks diving under semi-natural conditions. In experiments with non-diving birds, we were able to determine the profitability of different sized mussels.

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MATERIAL & METHODS

Mussels

Zebra mussels were collected weekly in lake IJsselmeer, The Netherlands, in November and December 1987. Mussels attached in clumps were detached from their substrate and separated by cutting the byssus. Dry weights (24 hours, 70 °C) and ash weights (90 minutes, 450 °C) were measured for 10 mussels per size class with shell lenghts of 3, 5, 7, 9, 11, 13, 15, 17, 19, 21, and 23 mm. Shell lengths were measured to the nearest mm. The relationship between ash-free dry weight of mussels including the shell (*AFDW*, g) and mussel shell length (*L*, mm) is described by the power function: $\log(AFDW) = 2.727 \log(L) - 5.007$; $r^2 = 0.992$.

Experiments without diving

Two hand-reared Tufted Ducks (a male and a female, body mass 450-500 g) were used in the experiments. The ducks were kept separately in cylindrical wire-netting cages. Room temperature was about 15° C. Food consisted of mixed grains and water ad lib. In addition, Zebra mussels were offered regularly to avoid possible alteration of the gastro-intestinal tract (Kehoe *et al* 1988). The experiments were carried out when the ducks were fully grown, at an age of 6 to 8 months.

Handling times were measured by offering a known number of mussels of one mm length class at a time in a dish with about 3 cm water. The birds were watched from behind a blind. Handling time, defined as the time between picking up and complete swallowing a mussel, was measured using a stopwatch with an accuracy of 0.1 s. Because sometimes mussels were taken rapidly in the flow of water sucked into the bill and thus processed simultaneously, handling time was also defined as the duration of a bout of continuous handling divided by the number of mussels taken. The number of mussels offered was varied in successive trials, thus ensuring a spread in the number of mussels taken in one bout. The experiments were carried out at different times of the day and never lasted longer than two hours. Mussels of different size classes were offered in a random order to exclude effects of satiation. The profitability of each size class was calculated as the gross intake of organic material (*AFDW*) per mussel of that size class per second handling time.

Selection of mussel sizes from a field population was determined by taking a random sample of 200 gram wet weight (400 to 500 mussels of known size). The mussels were offered in an oval dish (about 30 x 18 x 5 cm) containing water (3 cm). Foraging time was measured using a stopwatch with an accuracy of 0.1 s. The dish was removed regularly to measure the shell length (to the nearest mm) of all remaining mussels. Afterwards, the remaining mussels were offered again and foraging was continued. This procedure was repeated, until the ducks refused to consume more mussels.

Experiments under semi-natural diving conditions

Three Tufted Ducks (1 adult male, 1 adult female, and 1 subadult male, body masses varying between 500 and 680 g) were succesfully trained to dive for mussels. They were kept singly in cages fixed to a pontoon in an 8 m deep water-filled sandpit. Each cage was constructed of an iron frame with wire netting and consisted of a deep shaft (1 x 1 x 5 m deep). At the water surface the cages were enlarged by 0.5 m (0.5 m deep), to give a total swimming area of 1 x 1.5 m. A board (20 x 20 cm) was placed in the shallow part of the cage a few centimeters above the water for the birds to rest. Food was offered on a tray (1 x 1 m with upright edges of 15 cm) in the dive shaft. Diving depth was manipulated by changing the level of the tray. Three months before the experiments started the birds were placed in their cages and fed on mixed grains. Diving depth was increased steadily up to 5 m. Thereafter, the diet was gradually altered to mussels over 4 weeks. Each day around noon, the birds were weighed, the remaining mussels were collected and total wet weight was measured, a sample was drawn from which mussel sizes were later determined, and an entirely new batch of mussels of known wet weight was offered. The experiments were conducted in November and December under normal local winter conditions, with wa-

ter temperatures slightly above freezing (2-5 °C).

Size selection was measured by taking samples of 150-250 gram wet weight (about 300 to 800 mussels) drawn before and after one day of consumption. Mussel sizes were measured to the nearest millimetre. The consumption per size class was calculated from the total weight loss of mussels in the tray after 24 hours and the changes in frequency distributions of size classes (2 mm each). The birds proved to consume up to 2 kg wet weight of mussels per day. The level of depletion was manipulated by varying the amount of mussels on offer (offering a smaller amount resulted in a greater level of depletion). An amount of 10, 8, 6, 5, and 4 kg wet weight was offered at a depth of 1.25 m. Ten, 8, and 6 kg was offered at a depth of 2.50 and 3.75 m, and 10 and 8 kg at 5.00 m, sufficient for the ducks to maintain their body weights. Tests without ducks proved that no mussels were lost from the tray as a consequence of experimental handling or water movement, and that the inaccuracy of wet weight measurements influenced the estimated consumed fractions by less than 5%.

We used the selectivity index D as proposed by Jacobs (1974) for comparison of size selection under different conditions. D is a derivative of Ivlev's electivity index E and has the advantage of being not sensitive to changes in relative frequencies of the resource population as a consequence of consumption. If r is the relative frequency of a certain size class in the diet and p the relative frequency of that size class in the resource population, then: $D = (r - p)/(r + p - 2rp)$. Values of D are between -1 and 1. If $D > 0$ that size class is preferred, if $D < 0$ that size class is selectively neglected. Because mussels were unequally distributed over size classes (see Fig. 3), calculations of the selectivity parameter D would be inaccurate in the lower and higher end of the size class range. To minimize this problem, size classes were pooled as follows: 1-6 mm, 7-10 mm, 11-12 mm, 13-14 mm, 1416 mm, 17-20 mm, and 21-26 mm. Values of D were not significantly different between the three ducks for all size classes (ANCOVA, $F_2 = 1.33$, $P = 0.27$). Therefore, the data were lumped for further analyses.

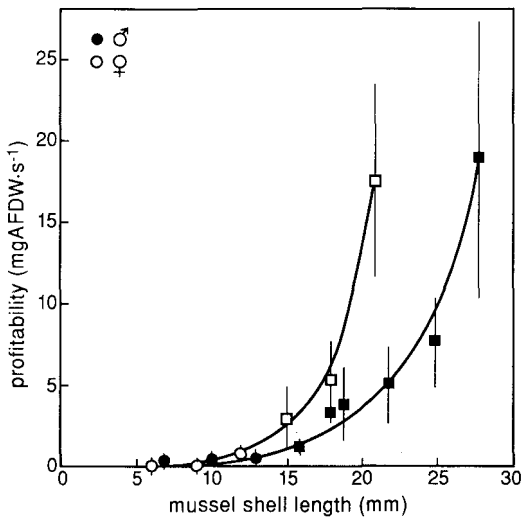

Fig. 1. Handling time per mussel (mean ± 1 *SD*) in relation to mussel shell length (open symbols female, closed symbols male; circles suction-feeding, squares picking).

RESULTS

Profitability in relation to mussel size and handling technique

Handling time increased with mussel shell length (Fig. 1). Mussels larger than 15 mm in the case of the female and 17 mm in the male were picked up individually. Much time was spent orienting the large mussels in the bill to achieve a suitable position for swallowing. Mussels larger than 18 mm in the female and larger than 25 mm in the male caused increasing difficulties and about one third of these larger mussels were rejected after being handled for 10-20 seconds. The largest mussels eaten were 25 mm for the female and 30 mm for the male. Mussels up to about 16 mm were taken up in bouts, i.e. a number of mussels was collected in the bill, before they were swallowed. These smaller mussels were collected in a water-suction-flow generated by rapidly repeated tongue movements. Tufted Ducks sieving mussels in this way resemble dabbling ducks filtering seeds from water (Kooloos *et al* 1989). The time spent handling mussels in a bout was linearly related to the number of mussels in that

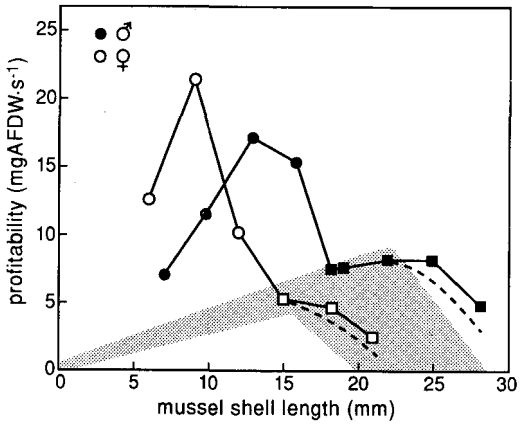

Fig. 2. Profitability curves of male and female duck (symbols as in Fig. 1). For comparison the range of profitability curves from Draulans (1984, 1987) is given (shaded area). Broken lines indicate profitability including rejected items.

bout. The slope of each line represents the mean handling time per mussel, as shown in figure 1.

The two size-related handling techniques greatly affect the profitability of the mussels (Fig. 2). The peaks of the curves reflect the high intake rate of small mussels in a suction-flow. In the male bird, a second peak seems to appear, representing the individually handled larger mussels. The average profitability of the largest mussels was in fact lower than indicated, because they were sometimes rejected. Draulans (1984, 1987) found the highest profitabilty for the largest mussels. The high peak for small mussels in our curves did not show up in the experiments undertaken by Draulans, who offered mussels without water. His birds did not have the opportunity to generate a waterflow and, consequently, the profitability of small mussels was much lower. For larger mussels the curves in the two studies are in good agreement. In conclusion, in the presence of water, feeding on small mussels sieved from a suction-flow is more profitable than picking up individual, larger mussels.

Preference for mussel size under non-diving and diving conditions

Size selection of mussels from field populations is illustrated for a male duck eating from a dish (non-diving) and one diving to 1.25 m (Fig. 3). In the non-diving situation, the duck apparently chose the smallest mussels on offer and gradually took larger mussels, when the smaller ones became scarce. In the diving situation, a wider range of mussel sizes was taken and a shift towards larger

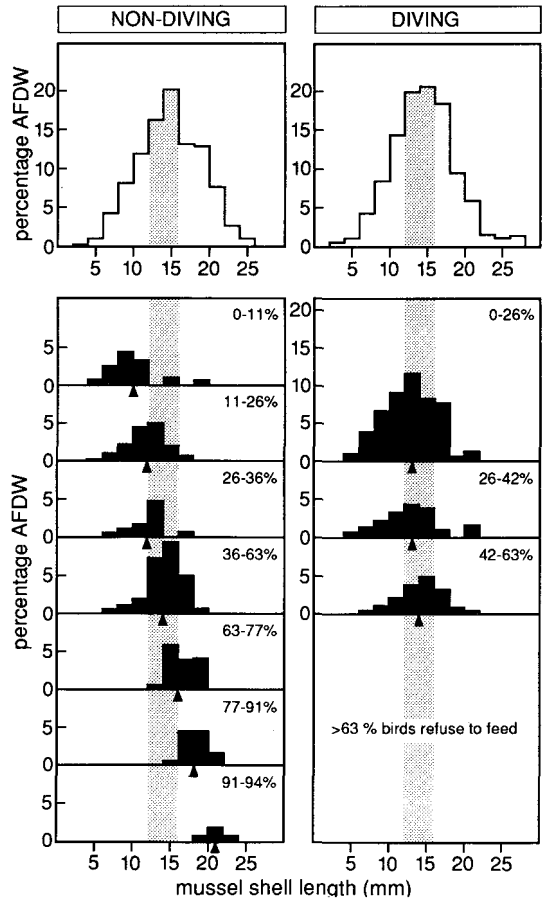

Fig. 3. Size selection from a field population of *Dreissena polymorpha* in a male duck in a non-diving situation (left) and a male duck diving to 1.25 m. The upper diagrams show the distribution of *AFDW* over size classes in the initial population (white). In the lower diagrams the fractions of *AFDW* taken from the initial population are shown in successive intervals of consumption (black) indicated by percentages. Triangles (▲) indicate the median mussel size per interval. Shaded areas show the most profitable size range (see Fig. 2).

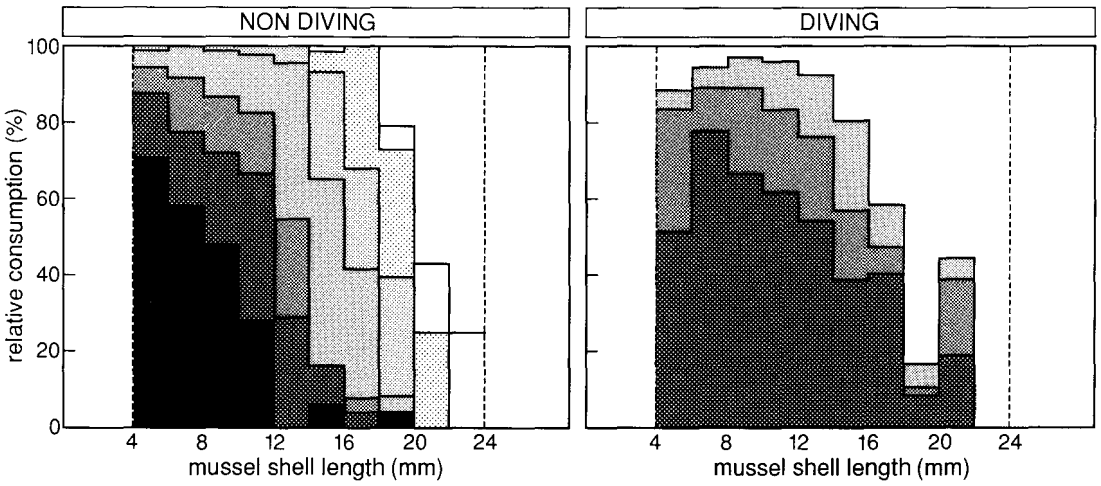

Fig. 4. Relative consumption of mussel sizes (cumulative percentages per size class) for a male duck in the non-diving situation (left) and a male duck diving to 1.25 m (right). Subsequent intervals of consumption (see Fig. 3) are ordered from dark to light.

mussels was not found. The relative consumption of size classes allows comparison of the two selection patterns (Fig. 4). The cumulative size distributions of the depletion intervals (computed on a *AFDW* basis) of 0-26% and 0-36% (0-42% in case of the diving situation), respectively, are significantly different between the non-diving and diving situation (Kolmogorov-Smirnov two sample test, $P < 0.001$ and $P < 0.05$, respectively), whereas the size distributions up to 63% (i.e. all small mussels are taken by suction-feeding in both situations) are not significantly different. Thus, in contrast to the clear shift from smaller to larger mussels in the non-diving situation, the diving bird continued to feed on all mussel sizes up to 16 mm. This pattern prevailed until almost all small mussels were taken. At that stage the diving subjects refused to eat more mussels. The same patterns were found in the other birds of the two groups (non-diving and diving, respectively), indicating that differences in selection are due to diving, indeed, rather than to individual differences.

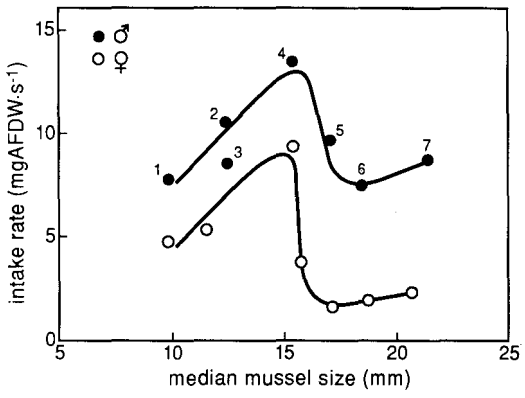

Fig. 5. Intake rates of mussels from a field population as a function of the median mussel size taken in successive intervals of consumption in the non-diving situation (● male, ○ female). Numbers correspond with successive intervals in Fig. 3 (left panel). Curves are fitted by eye.

In the non-diving situation, the intake rate of mussels changed along with the shift in mussel sizes taken (Fig. 5). Intake rates increased, when on average larger mussels were taken, up to sizes of about 16 mm, whereupon intake rates dropped to a much lower level. The sharp decline in intake rates coincides with a change in handling technique: when mussels that can be strained from a suction-flow become scarce, the intake of small mussels becomes less efficient, presumably because of the interference of the progressively more

abundant, larger mussels that must be picked up individually.

Selectivity under different diving conditions

Size selection under different conditions was compared by means of the selectivity parameter D (see Material and Methods). Linear regression analysis was used to determine whether resource depletion and diving depth influenced the selectivity for certain size classes. Resource depletion had no significant effect on the selectivity parameter D in all size classes ($P > 0.05$). Thus, the strategy of selection was independent of the abundance of the size classes, although the diving birds refused to eat when small mussels were no longer available (see Fig. 3). Selectivity was closely related to diving depth. A positive correlation was found for selectivity for the second, third, and fourth size class (7-10 mm, 11-12 mm, 13-14 mm, resp.; $P < 0.001$). Selectivity for the fifth size class (14-16 mm) was not related to diving depth ($P > 0.05$) and a negative correlation was found for the sixth size class (17-20 mm; $P < 0.05$). These relationships are illustrated in figure 6. There were no significant correlations with diving depth for the first (1-6 mm) and seventh size class (21-26 mm), probably because of the low numbers of mussels on offer.

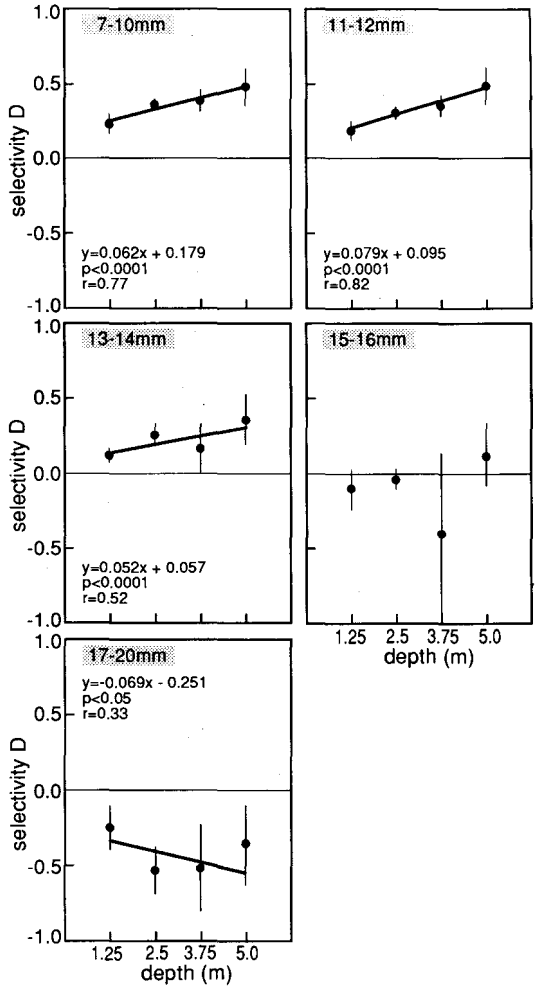

Fig. 6. Selectivity for different size classes in relation to diving depth (mean selectivity index $D \pm 1$ *SD*). Positive values of D indicate positive selection. Significant changes in selectivity are indicated.

Figure 6 also shows a marked switchpoint in selectivity for mussel sizes of 15-16 mm, which, again, coincides with the switchpoint in handling techniques (see Figs 2 & 5). In conclusion, the ducks became more selective towards the smaller mussels that could be handled in bouts when diving to greater depths. This suggests a shift in the proportion of feeding on small mussels, using the 'suction-flow' technique, relative to the 'pick-up' technique for larger mussels.

DISCUSSION

Profitability of suction-feeding

Small mussels proved to be most profitable in our study, due to the high intake rate of mussels by suction-feeding. The implications of this technique on foraging behaviour can be considerable, although several criteria have to be met to allow suction-feeding. Prey items must be small and occur in high densities and, of course, they must be obtained from water. Draulans (1982) found that Tufted Ducks preferred smaller prey sizes (10 - 15 mm) when he offered mussels in a ditch with turbid water, than when mussels were offered on the border of the ditch without water (15 - 20 mm most

preferred). Draulans believed that excluding visual cues in the former made the ducks choose conservatively smaller mussels in order to avoid the risk of taking mussels being too large to handle efficiently. Our data, however, show that the preference for smaller mussels can also be explained entirely by the higher profitability of small mussels, when obtained by suction-feeding in water.

Conditions of high densities of small, single food items are often met by diving ducks, for example in high densities of spat of *Dreissena polymorpha*, but also other food types, e.g. fry-eating Surf Scoters *Melanitta perspicillata* (Vermeer 1981) or Goldeneyes *Bucephala* spp. (Vermeer 1982). Pochard *Aythya ferina*, Scaup *A. marila*, Goldeneye, and Tufted Duck often feed on micro bivalves, *Pisidium* spp., small gastropods, *Hydrobia* spp., *Potamopyrgus* spp., benthic ostracods, or plant seeds (Madsen 1954, Olney 1963, Olney 1968, Nilsson 1972, own obs.). Thus, suction-feeding on small prey (< 5 mm) could be widespread. We believe that suction-feeding, as an alternative for consuming larger bivalve prey, opens up an extensive feeding niche for benthic feeding diving ducks.

Size selection and the costs of foraging

The selection patterns shown in figures 3 & 4 may indicate that Tufted Ducks select mussel sizes by indifferently accepting all mussels smaller than a certain threshold size. The opening at the bill-tip determines which prey sizes can enter the bill (Kooloos *et al* 1989) and thus sets the upper threshold of acceptance. In the non-diving situation, the ducks only accepted the smallest mussels available and the level of acceptance was raised in response to depletion of the smaller sizes. In the diving birds, the level of acceptance was fixed at a mussel size of about 16 mm, thus accepting all mussels that could be strained by suction-feeding. This foraging technique implies that small, less profitable mussels will also be sucked into the bill. Although small food items (diameter 2 mm) already grasped in the bill can be rejected concurrently with retaining larger items (Kooloos *et al* 1989, Ball 1990), it might be time consuming or impossible to reject mussels of about 7-10 mm while retaining the most profitable sizes of 10-15 mm. Therefore, rejection of the smallest size classes may be unprofitable when suction-feeding.

In the non-diving situation, the ducks initially took smaller mussels than the most profitable sizes (Figs 2 & 3). In the diving birds, however, the most profitable and most abundant sizes were also included in the diet. On average, the diving birds accepted larger prey than the non-diving birds. We found no individual differences within the two groups, suggesting that the differences in size selection were due to diving, indeed. Similarly, Ydenberg (1988) found that White-winged Scoters *M. fusca* feeding at the water surface chose smaller blue mussels *Mytilus edulis* than when diving. Could this be a general difference between diving and non-diving animals? And if so, what can account for this discrepancy? In many studies, where non-diving birds preyed on relatively large bivalve prey, smaller items than the most profitable sizes were favoured, for example in all experiments carried out by Draulans (1982, 1984, 1987) on Tufted Duck and Pochard. Profitability is measured as the gross energy intake per unit handling time. The proper rationale, however, would be the net energetic gain per unit handling time, thus subtracting the costs of foraging from the energy gain (Stephens & Krebs 1986). The preference for the smaller prey sizes is probably a consequence of the habit of crushing the mussels in the gizzard. The energetic cost for crushing is related to shell thickness, thus favouring smaller mussels. On the other hand, the gullet might operate most efficiently, when it is filled with a mixture of prey sizes, as Ydenberg (1988) proposed. This 'mixed bag' hypothesis could explain the consumption of a few larger mussels in addition to the favoured, smaller ones. This is best shown in the diving situation (Figs 3 & 4). However, an alternative hypothesis is available for taking additional large mussels by diving birds (see next section). It is interesting to note that size selection of Zebra mussels by the ciprinid fish *Rutilus rutilus* (which is not time constrained by breathing trips to the water surface) could be explained by the ratio of crushing resistance of mussel shells and the energy content of mussels of

different size (Prejs *et al* 1990). Bustnes & Erikstad (1990) found that the flesh content relative to shell weight of blue mussels decreased with mussel size and suggested that Common Eiders *Somateria mollissima* selected small sizes to minimize the daily intake of shell material. Thus, mussels smaller than the size category assuring highest intake rates may in fact be more profitable in terms of net energetic gain for the ducks in the non-diving situation.

Diving ducks have also to pay the costs of collecting food under water (the metabolic rate during submersion is about 3.5 the resting rate in the Tufted Duck, Woakes & Butler 1983), due to transit between surface and bottom and work to overcome buoyancy. An associated cost is the subsequent recovery period at the surface (again at 3.5 resting metabolic rate). The diving birds chose a diet in which all mussels up to 16 mm were included, thus increasing their intake rate. In doing so, the costs of collecting prey under water were minimized, but the birds accepted consequently higher costs of food processing (crushing shells and digestion) afterwards. The ducks in the non-diving situation interrupted foraging for about 10 minutes to unload the gullet by crushing the mussel shells, when approximately 15-20 g wet weight of mussels was taken. Based on this observation, diving ducks consuming about 1500 g wet weight each day may need up to 15 hours to process their food. Wild birds do not exceed 3 hours of diving time per 24 hours (Suter 1982). We believe that in general diving ducks minimize the time spent diving, thereby maximizing gross energy intake rate. Any extra time spent under water would increase the costs of foraging. The expected lower efficiency of crushing and digestion (e.g. Speakman 1987, Dade *et al* 1990) might be compensated by longer intervals between foraging bouts to process food, thus extending the period of foraging.

Foraging strategy in response to short dive times

Selectivity for the smaller size classes increased with diving depth and no effect of mussel density was found. These findings seem to contradict results of field experiments of Draulans (1982), who found less selective prey choice with increasing diving depth and lower densities of mussels. In the field experiments carried out by Draulans (1982), however, mussels were attached in clumps. Mussel sizes are unequally distributed in clumps (smaller ones closer to the edge) and clumps as a whole can be taken to the surface (own observations), limiting the choice of prey sizes. Thus, selectivity may depend on the number of mussels taken per clump, which in turn may depend on diving depth. Therefore, feeding on clumps is complicated and should be further studied.

Considering the way different sized mussels are handled according to our observations (small mussels up to 16 mm in a suction-flow versus picking up larger mussels), we may expect that these handling techniques are mutually exclusive (see Fig. 5). Handling large mussels may occur while surfacing, as is the case for example in mussel-feeding White-winged Scoter (Ydenberg 1988), Scaup (own observations) and Common Eider (Swennen 1976). Large mussels can be picked up at the bottom (one at a time) and handled at the surface without extra costs for diving. Draulans (1982), however, has already suggested that Tufted Ducks may prefer smaller sizes, when time at the bottom is limited, because several small items would yield more energy per dive than a single large food item. For species like Tufted Duck, adapted to take small prey, a functional strategy would be taking up small mussels in a run first and at the end, when bottom time is nearly over, pick up a larger one. The timing of taking a particular prey size can be explained in terms of lost opportunity (Stephens & Krebs 1986). Taking a large item at the beginning of a dive would prohibit taking any more mussels in a dive and is thus not the optimal strategy. Not taking a large item at the end of a dive is unprofitable, because no further diving costs are required to get the extra food item. Observations by means of a video-camera mounted just above the tray with mussels showed that Tufted Duck do indeed feed in runs and that larger items are taken to the surface (own obs.). It was also found that the time spent foraging at the bottom increased with diving depth. Wilson & Wilson (1988) regard diving birds as central-place-for-

agers (Orians & Pearson 1979) and predicted that diving birds should increase their foraging time under water at greater depths in order to use their dive time most efficiently. We suggest, therefore, that selectivity for small size classes increased with diving depth, because in deeper dives more time was spent to take small mussels in a run, before a large mussel was picked up.

Analyses of gullet contents of a variety of diving ducks, such as Goldeneye, species of the genus *Aythya*, Common Scooter *M. nigra*, and Eider, show that food items smaller than 10 mm are most frequently ingested (on weight basis), while most individuals consume few items larger than 15 mm (e.g. Madsen 1954, Olney 1963, Olney 1968, Nilsson 1972). This implies that observations on (large) prey handled at the surface are likely to underestimate both diet diversity and food intake rates.

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REFERENCES

Ball, J.P. 1990. Active diet selection or passive reflection of changing food availability: the underwater foraging behaviour of Canvasback Ducks. In: R.N. Hughes (ed.) Behavioural Mechanisms of Food Selection (NATO ASI Series G20): 95-107. Springer, Berlin Heidelberg New York.

Bij de Vaate, A. 1991. Distribution and aspects of population dynamics of the Zebra Mussel *Dreissena polymorpha* (Pallas 1771) in the lake IJsselmeer area (The Netherlands). Oecologia 86:40-50.

Bustnes, J.O. & K.E. Erikstad 1990. Size selection of Common Mussels *Mytilus edulis* by Common Eiders *Somateria mollissima*: energy maximization or shell weight minimization? Can. J. Zool. 68: 2280-2283.

Dade, W.B., P.A. Jumars & D.L. Penry 1990. Supply-side optimization: maximizing absorptive rates. In: R.N. Hughes (ed.) Behavioural mechanisms of food selection (NATO ASI Series G20): 531-556. Springer, Berlin Heidelberg New York.

Dewar, J.M. 1924. The bird as a diver. Witherby, London.

Draulans, D. 1982. Foraging and size selection of mussels by the Tufted Duck *Aythya fuligula*. J. Anim. Ecol. 51:943-956.

Draulans, D. 1984. Suboptimal mussel selection by Tufted Ducks *Aythya fuligula*: test of a hypothesis. Anim. Behav. 32:1192-1196.

Draulans, D. 1987. Do Tufted Duck and Pochard select between differently sized mussels in a similar way? Wildfowl 38:49-54.

Draulans, D. & A.F. De Bont 1980. Een analyse van het duiken naar voedsel van de Kuifeend *Aythya fuligula* buiten het broedseizoen. Gerfaut 70:251-260.

Jacobs, J. 1974. Quantitative measurements of food selection. A modification of the Forage ratio and Ivlev's Electivity index. Oecologia 14:413-417.

Kehoe, F.P., C.D. Ankney & R.T. Alikauskas 1988. Effect of dietary fiber and diet diversity on digestive organs of captive Mallards *Anas platyrhynchos*. Can. J. Zool. 66:1597-1602.

Kooloos, J.G.M., A.R. Kraaijeveld, G.E.J. Langenbach & G.A. Zweers 1989. Comparative mechanics of filter feeding in *Anas platyrhynchos*, *Anas clypeata* and *Aythya fuligula* (Aves: Anseriformes). Zoomorphology 108:269-290.

Kooyman, G.L. 1989. Diverse Divers, Physiology and Behavior. Springer, Berlin Heidelberg New York.

Lucas, J.R. 1990. Time scale and diet choice decisions. In: R.N. Hughes (ed.) Behavioural Mechanisms of Food Selection (NATO ASI Series G20): 165-185. Springer, Berlin Heidelberg New York.

Madsen, F.J. 1954. On the food habits of diving ducks in Danmark. Dan. Rev. Game Biol. 2:157-266.

Nilsson, L. 1972. Habitat selection, food choice, and feeding habits of diving ducks in coastal waters of South Sweden during the non-breeding season. Ornis Scand. 3:55-78.

Orians, G.H. & N.E. Pearson 1979. On the theory of central place foraging. In: D.J. Horn, R.D. Mitchell & G.R. Stairs (eds) Analysis of Ecological Systems: 154-177. Ohio State University Press, Columbus.

Olney, P.J.S. 1963. The food and feeding habits of Tufted Duck *Aythya fuligula*. Ibis 105:55-62.

Olney, P.J.S. 1968. The food and feeding habits of Pochard *Aythya ferina*. Biol. Cons 1:71-76.

Pedroli, J.C. 1981. Les relations entre la Moule Zebree *Dreissena polymorpha* et les oiseaux aquatiques. PhD thesis, University of Neuchâtel.

Prejs, A., K. Lewandowski & A. Stanczykowska-Piotrowska 1990. Size-selective predation by roach

Rutilus rutilus on zebra mussel *Dreissena polymorpha*: field studies. Oecologia 83:378-384.
Speakman, J.R. 1987. Apparent absorption efficiencies for Redshank *Tringa totanus* and Oystercatcher *Haematopus ostralegus*: implications for the predictions of optimal foraging models. Am. Nat. 130: 677-691.
Stephens, D.W. & J.R. Krebs 1986. Foraging Theory. Princeton University Press, Princeton.
Suter, W. 1982. Vergleichende Nahrungsökologie von überwinternden Tauchenten *Bucephala*, *Aythya* und Blässhuhn *Fulica atra* am Untersee-Ende/ Hochrhein (Bodensee). Orn. Beob. 79:225-254.
Swennen, C. 1976. Populatie-structuur en voedsel van de Eidereend *Somateria m. mollissima* in de Nederlandse Waddenzee. Ardea 64:311-371.
Vermeer, K. 1981. Food and populations of surf scoters in British Columbia. Wildfowl 32:107-116.
Vermeer, K. 1982. Food and distribution of three *Bucephala* species in British Columbia waters. Wildfowl 33:22-30.
Willi, P. 1970. Zugverhalten, Aktivität, Nahrungserwerb auf dem Klingnauer Stausee häufig auftretender Anatiden, insbesondere von Krickente, Tafelente und Reiherente. Orn. Beob. 67:183-217.
Wilson, R.P. & M.P.T. Wilson 1988. Foraging behaviour in four sympatric cormorants. J. Anim. Ecol. 57: 943-955.
Woakes, A.J. & P.J. Butler 1983. Swimming and diving in Tufted Ducks *Aythya fuligula* with particular reference to heart rate and gas exchange. J. Exp. Biol. 107:311-329.
Ydenberg, R.C. 1988. Foraging by diving birds. In: H. Ouellet (ed.) Acta XIX Congressus Internationalis Ornithologici (Vol. II): 1832-1842. University of Ottawa Press, Ottawa.

SAMENVATTING

In NW-Europa is de Driehoeksmossel het stapelvoedsel van overwinterende Kuifeenden en andere duikeenden. Kenmerkend voor duikeenden is de relatief korte tijd die dagelijks aan voedsel vergaren wordt besteed. In dit onderzoek is bij Kuifeenden gekeken hoe het duiken invloed uitoefent op de grootte van de gekozen mossels. Hiervoor werden drie eenden getraind om te duiken naar mossels, die tot een diepte van 5 m werden aangeboden in individuele duikkooien. Bij niet-duikende eenden werd de techniek en de efficiëntie van het selecteren van mossels van verschillende grootte waargenomen.

Uit deze experimenten bleek dat Kuifeenden gebruik maken van twee fourageer-technieken: kleine mossels (met schelplengte kleiner dan 16 mm) worden met meerdere tegelijk opgezogen en uit het water gefilterd, terwijl grotere mossels (17 tot 30 mm) individueel opgepakt en doorgeslikt worden.

Het filteren van kleine mossels is het meest efficiënt uit het oogpunt van voedsel-opname (uitgedrukt in asvrij drooggewicht, *AFDW*). De eenden die niet hoefden te duiken selecteerden de kleinst mogelijke mossels, vermoedelijk om de kraakkosten van de in hun geheel doorgeslikte mossels te beperken. De eenden die doken naar mossels waren minder selectief en verkozen het filteren van alle mossels kleiner dan 16 mm, terwijl daarnaast ook enkele grotere mossels werden gegeten. Hierdoor wordt waarschijnlijk de dagelijkse fourageertijd onder water geminimaliseerd.

Naarmate de eenden dieper doken werden relatief meer kleinere mossels gegeten. Deze schijnbare toename van selectiviteit voor kleine mossels kan verklaard worden uit een verschuiving in de verhouding waarin beide fourageer-technieken worden gebruikt: diep duikende eenden blijven per duik vermoedelijk langer op de bodem kleine mossels selecteren, voordat ze een grotere mossel meenemen naar het wateroppervlak, die daar (zonder extra duiktijd) kan worden ingeslikt.

De techniek van het efficiënt filteren van kleine benthische prooien, als alternatief voor het opduiken van grotere schelpdieren, stelt duikeenden in staat een breed scala van voedselbronnen te benutten.