Do Tufted Duck and Pochard select between differently sized mussels in a similar way?

DIRK DRAULANS

Introduction

Tufted Duck *Aythya fuligula* and Pochard *Aythya ferina* are related diving ducks which often form mixed flocks during the winter season (Draulans 1980; Pedroli 1981; Draulans 1982a; Suter 1982a; Zuur *et al.* 1983; Draulans 1985). While Tufted Duck are considered to prey almost exclusively on animal food, Pochard usually feed on plant material (Madsen 1953; Olney 1963, 1968; Bauer and Glutz von Blotzheim 1969; Cramp and Simmons 1977). Freshwater mussels *Dreissena polymorpha* provide an important food resource for wintering Tufted Duck mainly (Olney 1963; Bauer and Glutz von Blotzheim 1969; Draulans 1982b; Suter 1982b; Zuur *et al.* 1983), but, despite their largely vegetarian preferences, Pochard have also been reported to forage intensively on freshwater mussels at sites where these mussels are very abundant (Geroudet 1978; Pedroli 1981; Suter 1982a; Suter 1982b; Zuur *et al.* 1983). This raises the question of possible competition for food between both species of diving ducks at such sites, in particular as Tufted Duck have been shown to select a restricted range of mussel sizes only (Draulans 1982b).

A series of experiments with captive ducks was set up to find out whether or not under daylight conditions both species can visually select similar mussel sizes in a comparable way. Standard profitability curves were calculated to compare optimal mussel sizes between both species, and selection experiments were performed to test whether or not the ducks also preferred these optimal sizes, and selected between mussels in a comparable way.

Materials and Methods

The experiments were performed with three pairs of Tufted Duck, housed in outdoor fowl runs of 8 x 3 m, each crossed by a ditch of 0.8 m wide. Although initially also three pairs of Pochard were trained, only two males and one female survived the whole series of experiments. These birds were housed in 3 x 3 m fowl runs, each containing a pool of 1 m^2. All ducks were tested separately from each other. The mussels used were collected in the field immediately before the experiments, and assigned to size classes according to shell length. The smallest size class included all mussels of less than 5 mm length, but all subsequent classes covered 2.5 mm intervals only. The mussels were presented separately and spaced out randomly on the stony border near the edge of the water where the ducks were usually resting. The ducks, which were usually fed on cereals were trained to feed on *ad libitum* mussels for one week prior to the tests. They were fed on cereals again in between the tests.

Profitability of mussels for the ducks was calculated as energetic gain per unit handling time (Krebs 1978). This does not make allowance for the energetic costs of handling, which were assumed to be negligible. The energy content of mussels of different size classes was measured through bomb calorimetry (Draulans and Wouters in press), and handling times of individual ducks were recorded from less than 5 m distance using an electronic digital stopwatch. Handling was defined as the time between pick up and complete swallowing of a mussel (measured accurate to 0.01 sec for at least 30 mussels of each size class for each bird). Two types of selection experiments were performed, the first in which the ducks could select between 100 mussels (10 of each of the 10 size classes). After usually 10 mussels had been eaten the ducks were chased away, and the remaining mussels collected and measured to assess how many mussels of which size classes were taken by the ducks. Each bird performed this experiment at least three times. In a second experiment a pair of each species was faced with a series of trials in which 10 mussels of only two size classes were presented. Trials were repeated twice for each possible combination of two size classes and the ducks were allowed to take 10 mussels. Again, the remaining mussels were collected and measured to assess which sizes were taken.

Wildfowl 38 (1987): 49–54

Results

Profitability increased gradually with increasing mussel size for all birds until a maximum was reached (the optimum) after which a steady decrease was recorded (mainly as a consequence of the exponential increase of handling time with mussel size)

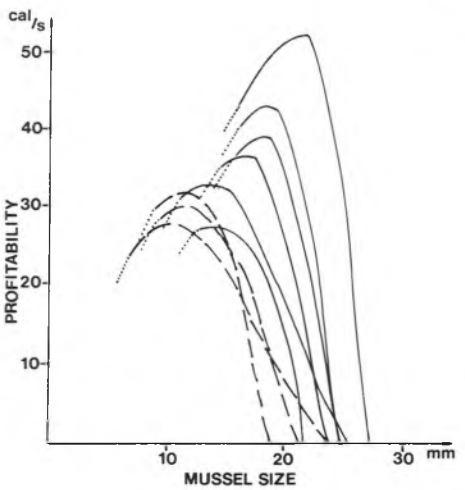


Figure 1. Profitability curves of six Tufted Duck (solid lines) and three Pochard (interrupted lines) feeding on freshwater mussels.

(Figure 1). The curves presented indicate large differences between all individuals tested, and include no-profitability data for the largest size classes (a nul was included in the calculations if a duck was unable to swallow mussels of a particular large size). The optimal mussel size was larger for Tufted Duck than for Pochard, and the optimal size turned out to be proportionally more profitable in the former species. The difference between optimal sizes for both species was approximately 5 mm, which is quite large (±25%) when compared to the actual range of mussels available to the ducks.

There were large individual variations in optimal mussel size within both the Tufted Duck and Pochard tested (in the range of about 7 mm for the six Tufted Duck and 4 mm for the three Pochard). These differences seemed not to be related to the size of the bill of the ducks (Figure 2). The Pochard, with on average a larger bill than the Tufted Duck, were even faced with

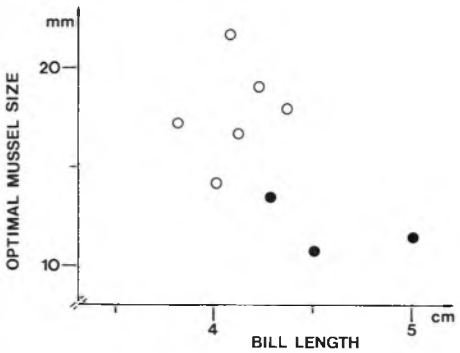


Figure 2. Relationship between optimal mussel size and bill length for Tufted Duck (white dots) and Pochard (black dots).

much smaller optimal mussel sizes than the latter, resulting in an overall, but non-significant decrease in optimal mussel size with bill length ($r=-0.49$, $P>0.1$). For the Tufted Duck separately, however, there was an increasing, but again non-significant trend in optimal mussel size with bill length ($r=0.43$, $P>0.1$). These data suggest that individual variability in "skill" in dealing with mussels could be important in determining the shapes of optimality curves. This, however, remains to be investigated. As far as the Pochard were concerned, there was certainly no "learning" of handling mussels during the course of the training: recorded handling times for mussels of different size classes before and after the initial training were very similar.

When faced with a number of mussels of each size class, Tufted Duck seemed to take mussels of between 7.5 and 27.5 mm, with a clear preference for mussels of between 15 and 17.5 mm, which is slightly smaller than the optimum (Figure 3). Overall, they preferred mussels smaller than the optimum, although the smallest ones were neglected. This is completely different from what was recorded for the Pochard, which seemed to select the smallest mussels. They took mussels of between 0 and 15 mm, but preferred the smallest ones, as a consequence of which they almost always swallowed mussels that were much smaller than the optimum. A frequency distribution analysis revealed highly significant differences between mussel sizes selected by both Tufted Duck and Pochard ($X^2=54.6$, $df=9$, $P<0.001$).

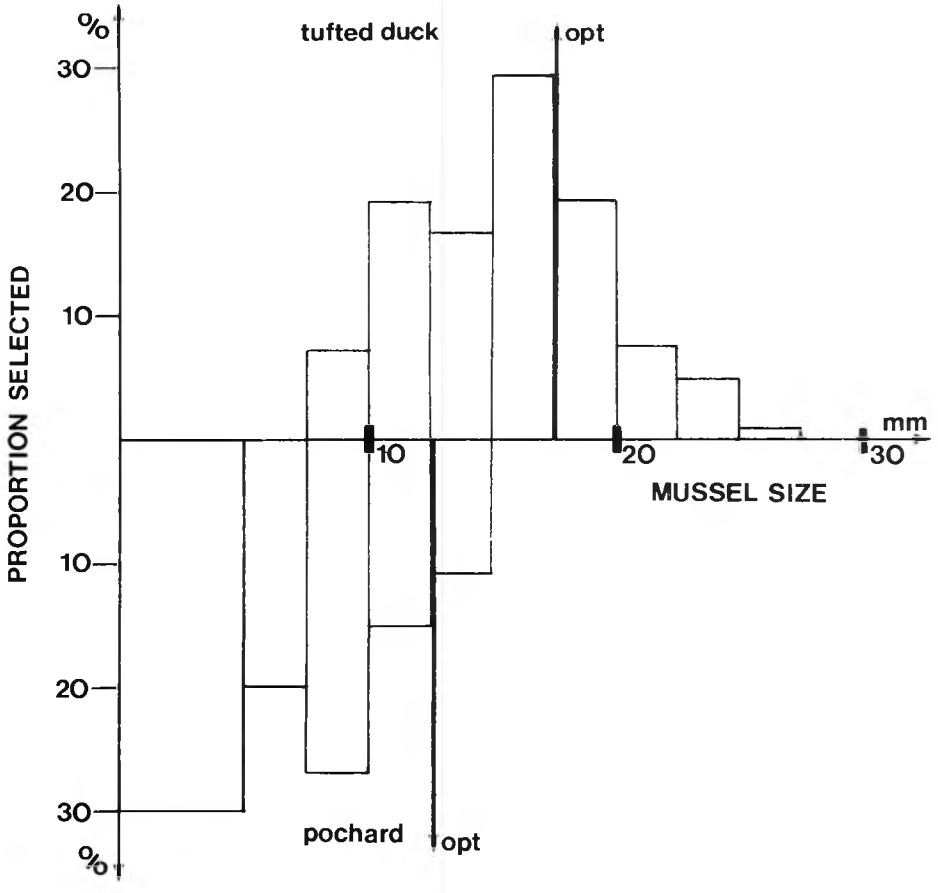


Figure 3. Selection of mussel sizes by Tufted Duck (upper half of the diagram) and Pochard (lower half of the diagram) in relation to the optimal mussel size (arrows) in a choice experiment with all size classes offered.

The data obtained in the second experiment, where the birds could choose only two mussel classes, stressed that Pochard almost always selected the smallest mussels, apart from three trials (11%) in which only two small size classes were offered (Table 1). The results for the Tufted Duck again were completely different: in slightly more than half the trials (52%) the birds preferred the largest musssels available. Apart from a few exceptions, Tufted Duck tended to avoid the largest mussels mainly when the alternative size class was not too small. So selection behaviour tended to be completely different for both species; Pochard taking preferentially smaller mussels and Tufted Duck preferentially larger ones.

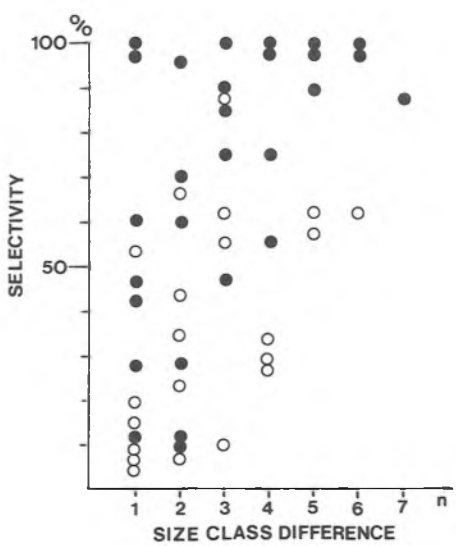
The discriminatory ability of Pochard is certainly not less than that of Tufted Duck (Figure 4). Pochard seemed able to select between mussels of less than 2.5 mm difference in length when it concerned the largest classes used. The larger the difference between the two size classes offered, the higher the probability that the birds were selective, but, as stated earlier, this does not imply that no selection was possible for the smallest range in difference. Although Tufted Duck also showed an increase in selectivity with increasing difference between the two mussel sizes offered, this increase was less impressive than that of the Pochard (100% selectivity was never recorded), and the Tufted Duck certainly did worse than the Pochard in the trials with only slight differences between size classes.

Table 1. Preference for mussel sizes by Tufted Duck (non-italic values) and Pochard (italic values) in two-choice experiments.

Least frequently selected mussel class	Most-frequently selected mussel class							
	(5–7.5)	7.5–10	10–12.5	12.5–15	15–17.5	17.5–20	20–22.5	22.5–25
(5–7.5)		*0.59*	*0.91*	*0.56*				
7.5–10		.		0.65	0.38	0.65		0.36
10–12.5		0.81/*0.52*	.	0.94	0.75	0.90	0.72	0.37
12.5–15		*0.88*	*0.90*	.	0.90			0.78
15–17.5	*0.43*	*0.25*	*0.40*	*0.71*	.	0.92		
17.5–20	*0.10*	*0.25*	*0.10*	0.92/*0.27*	*0.39*	.		
20–22.5	*0.00*	0.43/*0.00*	*0.00*	0.48/*0.12*	0.54/*0.30*	0.87/*0.00*	.	
22.5–25	*0.18*	*0.00*	*0.00*	*0.00*	0.11/*0.00*	0.34/*0.05*	0.46/*0.00*	.

( ): no experiments with this size class for the Tufted Ducks; values are the number of mussels of the least selected class divided by the number of mussels of the most selected class for each combination (averages for male and female; 0: complete preference for one class, 1: no preference for a size class); upper half of the table: tests where the largest mussels were preferred, lower half of the table: tests where the smallest mussels were preferred.

Figure 4. Selectivity by Tufted Duck (white dots) and Pochard (black dots) in taking mussels of a particular size class from two classes available in function of the difference between the two size classes offered.



Discussion

Sub-optimal mussel size selection by Tufted Duck has been shown earlier to occur when risks of taking mussels that are too large to be swallowed were high (Draulans 1984). As the proportion of unprofitable mussels was even higher for the Pochard in the experiments described here, one could predict sub-optimal selection by this species to be even more obvious than in the case of the Tufted Duck, which was indeed found. However, Pochard much more than the Tufted Ducks seemed able to discriminate between very similar large mussel sizes, which makes if difficult to withhold the "risk of taking unprofitable mussels" hypothesis, as this assumes the existence of discriminatory imperfectness. Discriminatory ability of the Tufted Duck seemed less developed than that of the Pochard, perhaps as a consequence of less pressure of Tufted Duck to make accurate distinctions, as they are able to handle a larger range of mussel sizes.

The preference of Pochard for very small mussels in our experiments was remarkable, and not in agreement with data from stomach analyses, where mussels of between 5 and 23 mm were reported for Pochard (Madsen 1953; Suter 1982b). However, using oesophagus food analysis (Pedroli 1981), the difference is not so high. From the nature of the experiments reported here it is certainly not the availability of different mussel sizes which can explain this discrepancy. It is possible that certain constraints of diving affect the pattern of size selection in the field. It must also be remembered that in field conditions the mussels are attached to the substrate and that depth and turbidity could affect the selection process. Moreover Suter (1982b) described Pochard and Tufted Duck as nocturnal and tactile feeders (which is

different from our experimental conditions) and taking the most abundant mussels (which were for the Pochard mainly what we calculated as the optimal ones). Tufted Duck, however, were shown to be selective in field experiments in a situation in which they were partly day-active (Draulans 1982b). Suter (1982b) also found Goldeneye *Bucephala clangula*, which were mainly diurnal, to have swallowed mussels of less than 5 mm length. The reason for this was attributed to the lack of sufficient musculature in their gizzard, making them unable to digest larger mussels. Pochard are, as stressed in the introduction, mainly plant feeders, and only occasionally take animal food exclusively. Partridge and Green (1985) summarised some evidence suggesting that on the one hand, digestive efficiency could be important in prey selection by animals, and, on the other hand, a switch in diet could cause a change in intestinal condition. It is assumed that the Pochard in the experiments selected the smallest mussels available to reduce some problems in digestion, as their gizzard musculature might not have been adapted to opening mussels, but that in situations in which animal food is predominant in their diet, they are able to deal with it properly. The data presented here particularly stress that analyses of profitability, based on "intake" measurements only, and selection, should be handled carefully if the "prey" concerned is one with which the predator is not familiar. The birds might have behaved "optimally" if other, for example digestive constraints could have been measured.

The experimental data indicated that even if Pochard and Tufted Duck forage together competition for mussels is minimal because of differences in size selection. Pochard are also often limited in their ability to exploit mussels as a consequence of their reduced diving capacities as compared to Tufted Duck (Bauer and Glutz von Blotzheim 1969; Willi 1970; Draulans and De Bont 1980). The very small mussels they selected contain little energy. It is, consequently, not surprising that Pochard are mainly vegetarian, and that in Belgium Pochard flock together with Tufted Duck during daylight only, but leave to forage on nearby channels at night, even though some of the roosting ponds house a rich freshwater mussel supply (Draulans 1985). However, in field conditions where mussels were very abundant (and other food limited?) Pochard seemed to adapt to this high food supply and swallow mussels of similar sizes to Tufted Duck, resulting in a high overlap in diet (Suter 1982b; Zuur *et al.* 1983). The abundance of mussels, however, probably prevents food competition from becoming important here; mussels stocks were never depleted completely (Pedroli 1981; Suter 1982c).

Acknowledgments

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Summary

A series of experiments with 6 captive Tufted Duck *Aythya fuligula* and 3 Pochard *Aythya ferina* was performed to test whether or not both species select between different sizes of mussel *Dreissena polymorpha* in similar way. Standard profitability calcuations indicated that the optimal mussel size was, on the average, a little smaller for Pochard than for Tufted Duck, despite the larger bill of the former. Both species selected sub-optimal mussel sizes, but, in contrast to Tufted Duck, Pochard tended to select the smallest mussels available. This led to a significant difference in mussel sizes selected between both species, which may reduce competition in the field. Experiments in which the ducks could select between only two mussel classes were presented. Pochard always took the smallest class. Tufted Duck, on the other hand, tended to select larger mussels, except in situations where both classes offered were proportionally large. Selectivity increased with the difference between mussel sizes available, but Pochard were able to discriminate between large mussels of less than 2.5 mm difference. It is argued that profitability calculations may lead to biased conclusions in situations where animals are faced with less familiar prey.

References

Bauer, K.M. and Glutz von Blotzheim, U.N. 1969. *Handbuch der Vogel Mitteleuropas Band 3: Anseriformes (2. Teil).* Frankfurt, Akademische Verlagsgesellschaft.

Cramp, S. and Simmons, K.E.L. 1977. *The birds of the Western Palearctic Volume I.* Oxford, Oxford University Press.

Draulans, D. 1980. Reduktie van kompetitie tussen tafeleend *Aythya ferina* L. en kuifeend *Aythya fuligula* L. *Wielewaal* 46:317–324.

Draulans, D. 1982a. Watervogels op de zandwinningsputten te Mol. Een synthese van winterwaarnemingen en tendenzen vanaf 1949 tot en met de winter 1980/81 *Wielewaal* 48: 90–106.

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

Draulans, D. 1984. Sub-optimal mussel selection by Tufted Ducks *Aytha fuligula*: test of a hypothesis. *Anim. Behav.* 32:1192–1196.

Draulans, D. 1985. The importance of large man-made waters in the north of Belgium for waterfowl. *Proc. 17th Congress of the International Union of Game Biologists*: 95–102.

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

Draulans, D. and Wouters, R. In press. Density, growth and calorific value of *Dreissena polymorpha* in a pond created by sand extraction, and its importance as food for fish. *Ann. Soc. Zool. Belg.*

Geroudet, P. 1978. L'évolution du peuplement hivernal des oiseaux d'eau dans le canton de Genève (Leman et Rhône) de 1951 à 1977. *Nos Oiseaux* 34:207–221.

Krebs, J.R. 1978. Optimal foraging: decision rules for predators. In: *Behavioural ecology: an evolutionary approach* (Ed. by J.R. Krebs and N.B. Davies), Pp. 23–63. Oxford, Blackwell Scientific Publications.

Madsen, F.J. 1953. On the food habits of the diving ducks in Denmark. *Dan. Rev. Game Biol.* 2:157–266.

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

Olney, P. 1968. The food and feeding habits of the Pochard *Aythya ferina. Biol. Conserv.* 1:71–76.

Partridge, L. and Green, P. 1985. Intraspecific feeding specializations and population dynamics. In: *Behavioural ecology: ecological consequences of adaptive behaviour* (Ed. by R.M. Sibly and R.H. Smith), Pp. 207–226. Oxford, Blackwell Scientific Publications.

Pedroli, J.C. 1981. *Les relations entre la moule zebree* Dreissena polymorpha *(Pallas) et les oiseaux aquatiques.* Neuchatel, Ph.D.-thesis.

Suter, W. 1982a. Die Bedeutung von Untersee-Ende/Hochrein (Bodensee) als wichtiges Uberwinterungsgewässer für Tauchenten *(Aythya, Bucephala)* und Blashuhn *(Fulica atra). Ornith. Beob.* 79:73–96.

Suter, W. 1982b. Vergleichende Nahrungsökologie von Überwinternden Tauchenten *(Bucephala, Aythya)* und Bläshuhn *(Fulica atra)* am Untersee-Ende/Hochrein (Bodensee). *Ornith. Beob.* 79:225–254.

Suter, W. 1982c. Der Einfluss von Wasservögeln auf Populationen der Wandermuschel *(Dreissena polymorpha Pall.)* am Untersee/Hochrein (Bodensee). *Schweiz. Z. Hydrol.* 44:149–161.

Willi, P. 1970. Zugverhalten, Aktivität, Nahrung und Nahrungserwerb auf dem Klingnauer Stausee häufig auftretender Anatiden, insbesondere von Krickente, Tafelente und Reiherente. *Ornith. Beob.* 67:141–217.

Zuur, B., Suter, W. and Krämer, A. 1983. Zur Nahrungsökologie auf dem Eundinger Becken (Bodensee) Überwinternder Wasservögel. *Ornith. Beob.* 80:247–262.

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