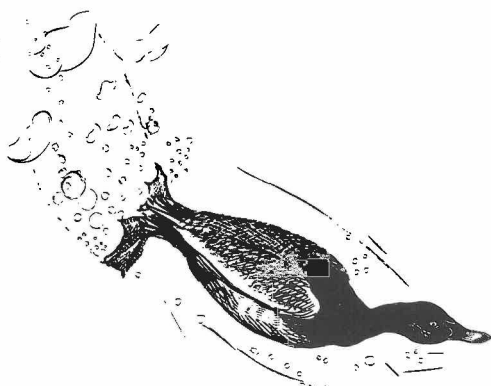


Guidelines for estimating the feeding performance of diving birds

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A method of assessing the feeding performance of wild diving birds is presented that relies on the use of field data on diving behaviour and environmental conditions, and of additional information on underwater behaviour obtained from captive diving experiments. Two components of feeding performance are considered - diving efficiency (measured as the ratio of the time spent feeding over the dive cycle time) and the rate of food consumption. These two components can be used to assess habitats that differ both in water depth and food concentration. At present, however, there is limited information available on consumption rates of birds feeding on natural foods and on different substrates in the benthos. This information could be obtained from captive feeding trials.

Keywords: *Pochard, Tufted Duck, Diving Behaviour, Foraging*

It has long been recognized that the feeding performance of diving birds is influenced by environmental factors such as water depth, food density and the depth of substrate covering the food (Dewar 1924, Draulans 1982). However, because our knowledge of diving birds is hampered by an inability to conduct underwater observations, we have a poor understanding of the degree to which these factors influence the birds' ability to feed. Such an understanding is important because it allows us to assess the resources available to diving birds, and may ultimately improve our understanding of their distribution in wetlands.

Recent studies on captive diving birds have provided a unique opportunity to improve our understanding of underwater behaviour because it has been possible to view the birds directly (or to monitor their movements) while they fed under a range of underwater conditions (Draulans 1982, 1984, Tome 1988a, 1988b, 1989, Ball 1989, De Leeuw & Van Eerden 1992, Lovvorn *et al.* 1991, Carbone & Houston 1994, Carbone *et al.* in press). Some of the information obtained from these studies would be of value to field studies of diving birds.

In this paper, I present a method for assessing feeding performance of wild diving birds. The method relies on the use of field data on diving behaviour and environmental conditions at the study site, and on additional data on underwater behaviour obtained from captive diving experiments. The estimate of feeding performance is based on two components - diving efficiency (discussed below) and rates of food consumption. This measure can be used to assess feeding sites that differ in water depth, food density, prey type and substrate condition. The method proposed differs from that used in some earlier studies, and I review data from two studies, Carbone & Houston (1994) and Carbone *et al.* (in press), to illustrate the advantages of the present method.

Methods

As the data presented here are used only for the purposes of review, the methods are only briefly outlined. For a more detailed description, see Carbone & Houston (1994) and Carbone *et al.* (in press). Data

presented in this paper are obtained from the Pochard *Aythya ferina* and the Tufted Duck *A. fuligula*. The experiments were conducted in two large aquariums with depths of 3.0 and 5.5 m. Food trays of approximately 1 m² were suspended within the aquarium and these could be adjusted to a range of water depths (**Figure 1**). During the experiments, the birds fed on mealworms, which were divided into roughly equal amounts, placed in four 45 cm² sub-trays and covered with sand. These trays were placed in the main tray and submerged. At the end of each trial, the remaining mealworms were sifted from the sand and counted. The amount remaining was deducted from the original number to calculate the number consumed. With a knowledge of the total time that the bird had spent feeding in the tray (see below) and the number of mealworms consumed, it was possible to determine the average rate of food consumption (mealworms per second at the food tray).

In a majority of the experiments, the birds fed individually (although data on birds feeding in groups are also presented, see Carbone *et al.* in press). The underwater behaviour of the birds was monitored by observation through glass panels at the side of the tank, or by the use of an underwater hydrophone (see Carbone & Houston 1994).

The dive cycle, as defined in this paper, includes both the dive and surface time (the time recovering on the surface between dives). Dive time is subdivided into foraging (beginning at the point where the bill touches the substrate and ending when the bill leaves the substrate) and total travel time (including the descent and ascent). Surface times of greater than 20 seconds (Carbone & Houston 1994) or 35 seconds (Carbone *et al.* in press) were considered as non-feeding activity and were excluded in the analysis (see discussion below concerning maximum surface times).

Three sets of experiments are referred to in this paper. Water depth experiments were designed to assess the effects of depth on the time available for feeding. The ducks were fed at a range of depths (up to 5.5 m) at 0.5 metre intervals.

Food concentration experiments were designed to determine the effect of concentration on the rate of food intake. These experiments were conducted on the Pochard only. Densities of 125, 375 and 500 mealworms/m² were used (Carbone & Houston 1994).

Sand depth experiments were designed to estimate the effect of the depth of substrate covering the food on consumption rates. Sand depths of 1.25, 2.5 and 3.75 cm were used (Carbone & Houston 1994).

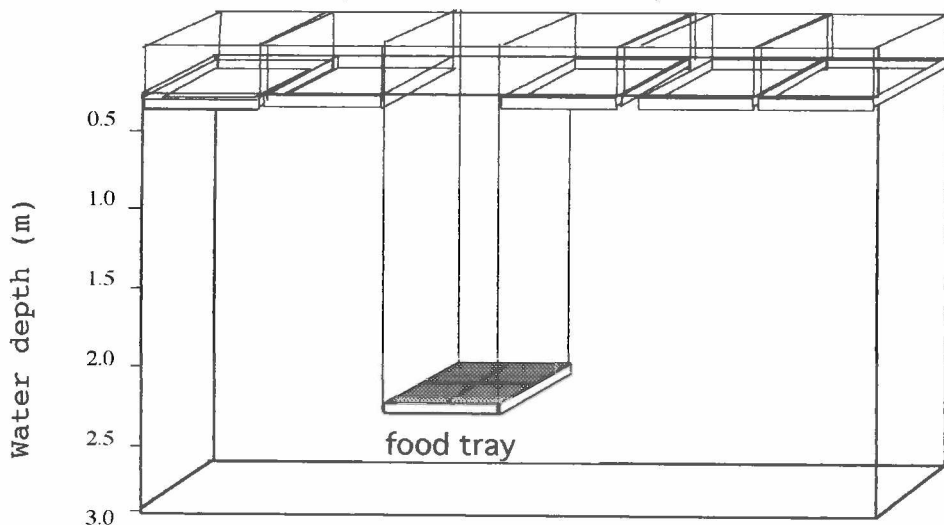


Figure 1. The diving tank used in Oxfordshire. From Carbone & Houston (1994).

Discussion

Patterns in the dive cycle

In order to provide a better understanding of diving behaviour, some typical patterns in diving behaviour in relation to water depth are summarised below. Carbone & Houston (1994) and Carbone *et al.* (in press) found that for the Pochard, the duration of each stage of the dive cycle changed with water depth (**Figure 2 a-d**). Dive duration increases with water depth due to an increase in both travel and foraging time. Travel time increases linearly with water depth, suggesting that travel speed is constant. Foraging time increases with water depth until it approaches maximum dive depth and then it begins to decrease to compensate for increasing travel time (Houston & Carbone 1992, Carbone & Houston 1994). Finally, surface time increases roughly in proportion to depth, but accelerates rapidly near the maximum diving depth. The upturn in

surface time is more noticeable in data from Nilsson (1972) and Carbone *et al.* (in press). The patterns in surface and foraging time can be explained using optimal foraging theory (see Kramer 1989, Houston & Carbone 1992, Carbone & Houston, in press, for a detailed explanation).

It is interesting to note that the observed patterns in the dive cycle are typical of patterns seen in other diving birds and in a broad range of diving animals (see e.g. Dewar 1927, Dolphin 1988, Kooyman 1988, Boyd & Arnborn 1991, Croll *et al.* 1992).

Previously used measures of diving efficiency

Previous field studies on diving behaviour have used the ratio of the dive duration over the time spent on the surface (dive time/surface time) and the proportion of time underwater (dive time/[dive time + surface time]). One problem with these measures is that the dive duration includes both foraging and travel time, and

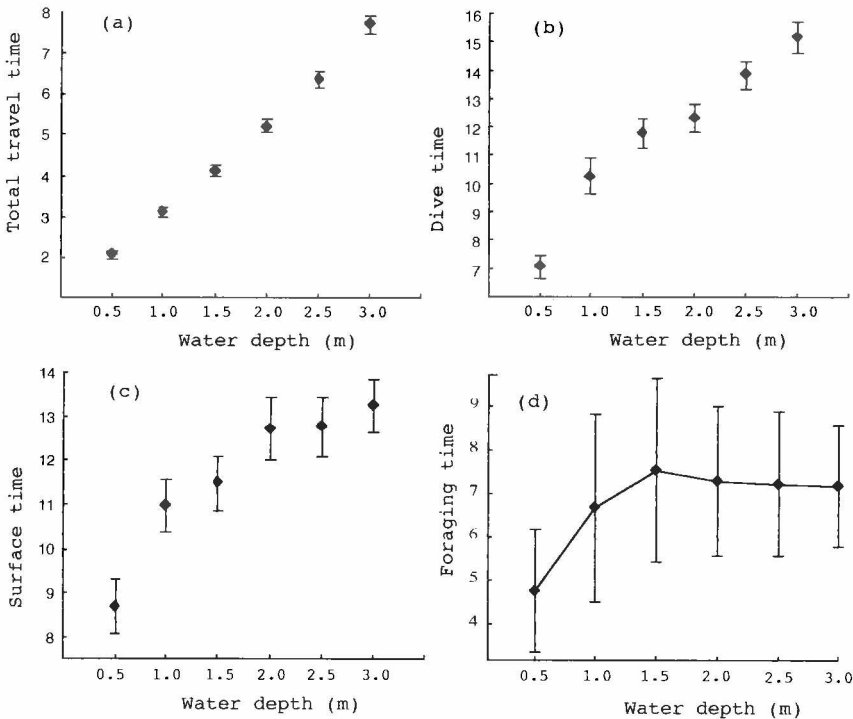


Figure 2. Patterns in the Pochard's dive cycle. a) Travel time, b) dive time, c) surface time and d) foraging time (in seconds) against the water depth (metres). Each point represents the mean ($\pm$ s.e.) of 16 birds. From Carbone & Houston (1994).

these two factors have a confounding effect. Ideally, it would be best to measure the time available for foraging relative to the dive cycle duration, and this is given by the proportion of time foraging (see equation 1 below).

To illustrate this point, data from Carbone & Houston (1994) and Carbone *et al.* (in press) were converted into the diving efficiency measures, the dive-surface ratio and the proportion of time underwater (Figure 3 a-d). These measures produce very different results. Diving efficiency appears to increase with water depth in the Carbone & Houston (1994) data set, but peak at around 2.5 m in the Carbone *et al.* (in press) data set.

When these data are converted to the diving efficiency measure, the proportion of time foraging, both sets show similar trends, with the proportion declining with increasing water depth (Figures 4 a and b). One would expect that diving

efficiency would decrease with depth because of the costs of increased travel time and of increased time spent on the surface recovering.

Estimating the proportion of time spent foraging

It is possible to estimate the average foraging times of a diving bird feeding in the wild using information about water depth and underwater travel speed. This requires the use of depth markers at the site of observation (see e.g. Dewar 1927, Draulans 1982). Information about travel speeds can be obtained from a number of captive diving bird studies (Lovvorn *et al.* 1991, Carbone & Houston 1994, Carbone *et al.* in press). These can provide an accurate estimate of travel time for a given depth. The regression equations for estimating travel time from water depth for Pochard and Tufted Duck are given below:

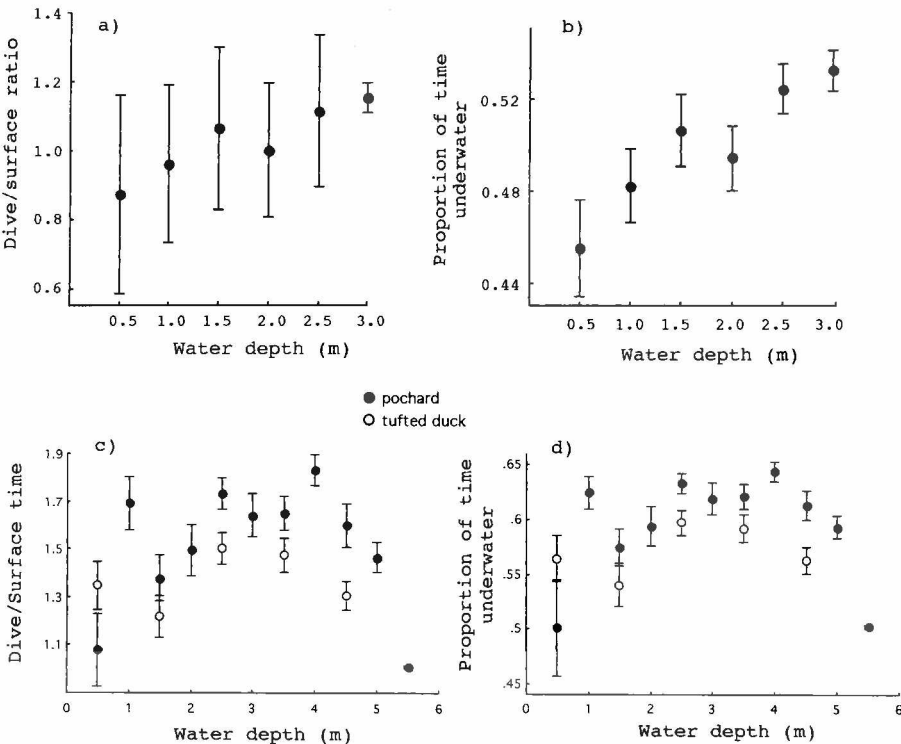


Figure 3. Previously used measures of diving efficiency against water depth (m), (means $\pm$ s.e.): Data calculated from Carbone & Houston (1994), Pochard, a) dive-surface ratio and b) the proportion underwater. Each point represents the mean ($\pm$ s.e.) of 16 birds. Data collected from Carbone *et al.* (in press), Pochard (seven birds), Tufted Duck (12 birds), c) dive-surface ratio and d) the proportion underwater.

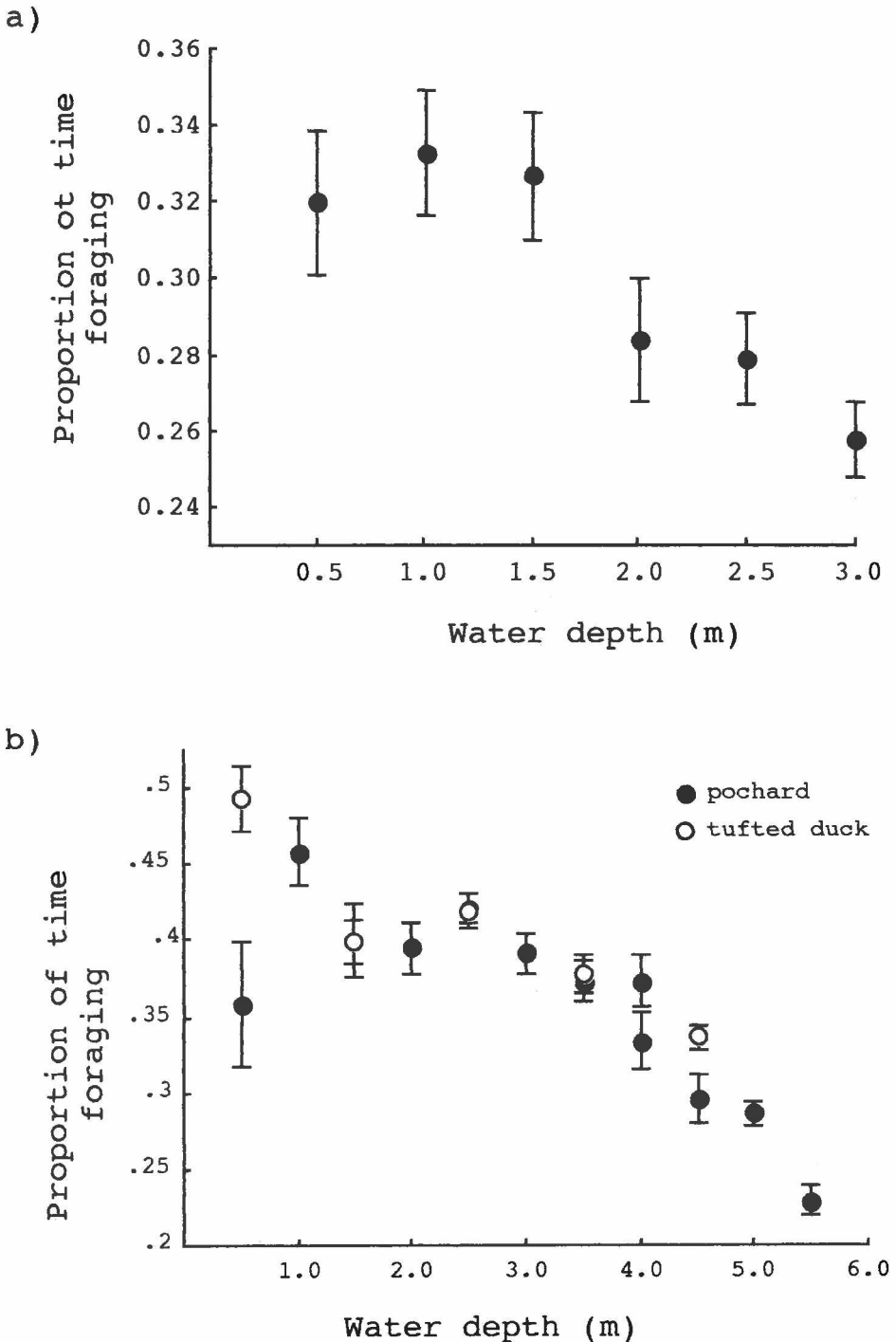


Figure 4. The proportion of time foraging against water depth (m) (means $\pm$ s.e.). a) Data calculated from Carbone & Houston (1994), Pochard. Each point represents the mean ($\pm$ s.e.) of 16 birds. b) Data from Carbone *et al.* (in press), Pochard (seven birds), Tufted duck (12 birds).

a) $Y = 2.24X + 0.84$, ($n=96$, $R^2=0.91$: Pochard, Carbone & Houston 1994),

b) $Y = 2.34X + 0.06$, ($n=60$, $R^2=0.95$: Tufted Duck, Carbone *et al.* in press),

where Y equals the total travel time in seconds, and X equals water depth in metres.

One can then estimate foraging time by subtracting estimated travel time from the dive time. The proportion of time foraging can be calculated by dividing the estimated foraging time by the dive cycle duration:

$$1) \frac{\text{foraging time}}{\text{foraging time} + \text{travel time} + \text{surface time}}$$

Maximum surface duration.

In order to estimate mean surface times from diving data, the maximum surface time that will be considered as part of feeding activity must be decided. This is because surface times can include activities other than that spent recovering from the dive (e.g. long bouts of preening, aggression and rest between feeding bouts). I recommend recording all surface times of 60 seconds or less (60 s is much longer than needed for recovery) and then using an objective method for estimating the maximum surface

duration from these values, e.g. estimating the bout criterion interval through the use of a log survivorship curve (see Martin & Bateson 1989, Boyd & Croxall 1992). This method allows the separation of long surface periods from normal length surface times in which the predominant activity is recovery for the next dive. On the other hand, one could use an arbitrary value (e.g. 35 s) based on former studies (see e.g. Ydenberg & Forbes 1988, Carbone *et al.* in press).

Rates of food consumption

The rate of consumption (items/foraging s) represents another important component of feeding performance. Carbone & Houston (1994) found that both food concentration and substrate depth influenced the rate of consumption (Figure 5 a and b). These relationships were strongly linear. Giles (1990) also found a linear relationship between food density and consumption rates in his study of Tufted ducklings feeding on chironomid larvae Chironemidae. Because of the consistency of these results, it should be possible to estimate consumption rates of birds at food densities that were not tested in the experiments from the

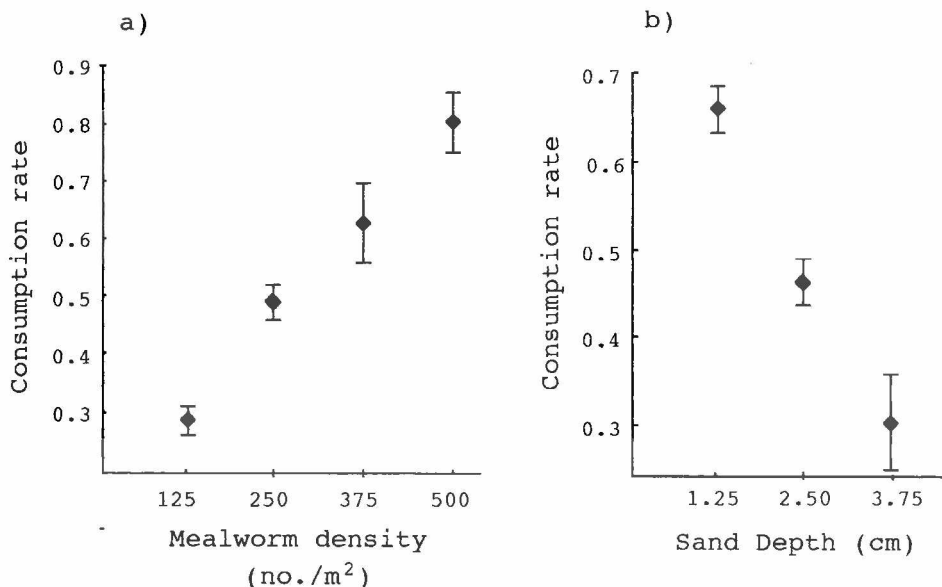


Figure 5. The rate of consumption by Pochard (mealworms/foraging s) (mean $\pm$ s.e.) against a) mealworm concentration (mealworms per m²) (eight birds) and b) sand depth (cm) (12 birds). From Carbone & Houston (1994).

equation of a linear regression analysis.

The consumption rates presented in Carbone & Houston (1994), however, were obtained from Pochard feeding on mealworms buried in sand. These conditions do not represent a natural food or substrate for this species and so the rates of consumption will differ considerably from Pochard feeding in the wild. However, captive studies with natural prey and substrate conditions can provide a reliable means of estimating rates of consumption of wild diving birds (see e.g. Draulans 1982, 1984, 1989, 1990, de Leeuw & Van Eerden 1992, and also, Tome 1988a, 1988b, 1989, Ball 1989 for semi-natural conditions).

At this stage, however, additional feeding experiments are needed to provide a better understanding of consumption rates in wild birds. Such experiments could be done with relatively simple, shallow tanks and with limited accessory equipment (see e.g. Draulans 1982, 1984). However, ideally, one should obtain estimates of consumption rates over a range of prey types, prey densities and substrate conditions. With measured prey densities and substrate conditions in the field, it is then possible to estimate the approximate consumption rates of wild birds.

Estimating the gross rate of intake

The two components of feeding performance, the proportion of time foraging and the rate of consumption can be determined separately for a given area of the study site. The product of these components can then be used to calculate the gross rate of intake (food items/dive cycle s). In for instance, 2), this calculation is presented showing each component of the dive cycle.

2)

$$\frac{\text{foraging time}}{\text{foraging time} + \text{travel time} + \text{surface time}} \times \frac{\text{no food items}}{\text{foraging time}} = \text{gross rate}$$

Because this measure includes both the measure for diving efficiency and food intake, it can be used to assess habitats that differ in both water depth and food concentration (also substrate conditions)

and is, therefore, a very convenient measure for assessing the overall feeding performance of divers (Carbone 1992, Houston & Carbone 1992).

Example from Phillips 1991

In a study on the feeding ecology of the Pochard, Phillips (1991) concluded that prey concentrations were the most important factor affecting feeding site preference. The Pochard were distributed non-randomly at the site, with 77% being located in less than 6.3% of the lake. However, as the preferred sites had both higher chironomid densities (preferred site density: 2890 chironomid larvae/m²; lake average density: 2388 chironomid larvae/m²), and shallower water (preferred site depth: 1.56 m; lake average depth: 2.28 m), it is not clear which of these factors most influenced preference. Using estimates of the proportion of time foraging at 1.5 and 2.0 m, of 0.33 and 0.28 respectively (Carbone 1992), one would expect a reduction of approximately 15.0% when foraging in areas of average depth rather than preferred regions. Using estimates of consumption rate from Giles (1990), average sites provide a 21.5% lower consumption rate (preferred site: 2.0/dive, lake average: 1.57/dive). These calculations suggest that prey concentrations are the most important factor influencing the gross rate of intake in this example, although water depth also has a substantial influence. The overall difference in gross rate between the preferred and remaining areas is estimated to be approximately 34.0%. It should be noted, however, that I was unable to use the exact method presented in this paper for the above example, because the appropriate data were not given in Phillips (1991) and Giles (1990).

Limits to this approach

Assumption of constant travel speed

The method which involves estimating travel time assumes that travel speed is constant. While this appears to be a reasonable assumption under most conditions and is found to be the case for a number of divers (Dolphin 1988,

Boyd & Arnborn 1992, Carbone & Houston 1994), recent evidence suggests that ascent speeds may be affected by environmental factors such as water temperature and buoyancy (Carbone *et al.* in press). Observed changes in travel speed are small, however, and probably only cause slight error in the estimates of travel time.

Food types

Consumption rates will be difficult to estimate if birds feed on a number of different food types at one site. This is because consumption rates will differ with food type and the birds may exhibit different preferences for different foods. In such circumstances, it may be necessary to conduct more elaborate experiments with mixtures of food types offered at different densities (see e.g. Draulans 1982, 1984, Ball 1989, de Leeuw & Van Eerden 1992).

Different diving strategies

Diving strategies may change considerably depending on the type of food that the diver feeds on (Carbone 1992). The approach suggested above would be most effective with divers which feed on several (three or more) items during a dive, for example, Pochard feeding on chironomid larvae or Tufted Duck feeding on small Zebra Mussels *Dreissena polymorpha*. Some divers may take only one prey item per dive, so foraging ends as soon as an acceptable item is found (Beauchamp *et al.* 1992, Nolet *et al.* 1993). In other divers, such as grebes Podicipedidae, which feed on fish, diving times are influenced by the short term changes in the availability of prey (Ydenberg & Forbes 1988, Ydenberg & Clark 1989). In addition, these species may not feed at the benthos (underwater floor) and so travel time may be difficult to estimate accurately. In the last case, the patterns of behaviour would be more complex and may require a different approach.

Importance of this approach

While captive bird studies are useful for

gaining a detailed understanding of diving behaviour (e.g. travel times and rates of consumption), field studies can provide us with an understanding of diving behaviour under a broader range of environmental conditions.

There are a number of areas which would be particularly useful to investigate using the technique described above. Harper (1982) found, in a series of experiments, that Mallards *Anas platyrhynchos* tended to distribute themselves in accordance with the amount of resource available as predicted by ideal free distribution models (Fretwell & Lucas 1970). Using the technique described above, one could determine whether the gross rate of intake was a good predictor of the distribution of diving birds.

One factor influencing both feeding rates (see above, also Draulans 1982, 1984) and the dive cycle (Carbone & Houston 1994, Carbone *et al.* in press) is substrate condition. However, at present we have a poor understanding of how substrate conditions influence feeding site preferences (but see, Draulans 1982, 1984, Giles 1989).

Several studies have identified sex differences in the duration of dives and time spent on the surface (Bauer & Glutz von Blotzheim 1969, Nilsson 1972, Draulans 1982, Pedroli 1982, Reynolds 1987). Carbone (1992) has also noted seasonal differences in the mean dive and surface durations. However, without an assessment of the proportion of time spent foraging, it is difficult to say whether these differences represent substantial sex differences in feeding performance. Field data which used the techniques described here would improve greatly our understanding of this issue.

Conclusion

A method for assessing feeding performance in wild diving birds is presented. Feeding performance is measured by the gross rate of intake as represented by the number of food items per dive cycle second. This can be calculated from the product of the proportion of time foraging and the rate of food consumption. Our

understanding of feeding ecology of divers would be improved greatly by a knowledge of either of these components. The method suggested requires the use of information about travel speeds and consumption rates from captive studies, and of information on water depth, prey density and

substrate conditions at the study site. At present, there are limited data available on consumption rates of natural prey and substrate conditions. More experiments in captivity on the rates of consumption will be required before we can estimate intake rates in wild diving birds reliably.

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