Foraging behaviour of wild Tufted Duck *Aythya fuligula* in winter

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Abstract

The Tufted Duck *Aythya fuligula* is invariably an underwater feeder which exploits the benthos. Field observations made in the early 20th century found that Tufted Duck foraging in the wild had a dive to surface time ratio of approximately 2 : 1. More recent studies of captive Tufted Duck found that the dive to surface time ratio was about 1 : 1. This study re-examined the feeding behaviour of wild Tufted Duck wintering in the UK. Mean water temperature at the benthos was 6.2°C (s.d. ± 1.6°C) over the study period. The mean dive times of 23.4 s (± 2.5 s) for males and 22.2 s (± 1.6 s) for females were significantly greater than the mean between-dive surface times of 10.7 s (± 1.6 s) and 10.4 s (± 1.6 s) for males and females, respectively. The corresponding mean dive to surface time ratios were 2.3 : 1 (± 0.3) for males and 2.2 : 1 (± 0.3) for females. Both measures were significantly greater than the mean dive to surface time ratio of 1.1 : 1 (± 0.2) reported for freely foraging captive Tufted Duck in diving physiology studies.

Key words: dive cycle, foraging, time budget, wild Tufted Ducks, winter temperatures.

In the wild, Tufted Duck *Aythya fuligula* invariably dive to take food on the benthos. High energy demands are imposed as a result of immersion and feeding in water, which can approach freezing (de Leeuw *et al.* 1998). Although Tufted Duck were shown to forage nocturnally in Central Europe (Pedroli 1982), in the UK they also forage diurnally. An early study of day-time feeding reported that wild Tufted Duck feed most frequently at depths of between 0.3–1.8 m, with dive times of about 16 s. The duration of the dive times increased with increasing water depths, and dive times were also found to be of longer duration than surface times, with dive to surface time ratios ranging from 1.8 : 1 – 2.4 : 1 (Dewar 1924). More recent studies of the diving physiology of Tufted Duck, where captive ducks feed freely in tanks or semi-submerged cages and take food from trays at defined depths, also measured dive and surface times. These indicated that dive time increased with increasing depth, and that surface time increased proportionally, with the ratio of dive to surface time at depths of

1–3 m remaining close to unity (Carbone *et al.* 1996; Halsey *et al.* 2003a; Halsey *et al.* 2003b; de Leeuw *et al.* 1998; Parkes *et al.* 2002; Woakes & Butler 1983). It has been suggested that the difference between captive and wild Tufted Duck in their feeding activity may be partly attributable to the absence of competition when captive ducks feed in isolation (Halsey *et al.* 2006).

Laboratory investigations of the physiological factors limiting underwater foraging have studied both respiratory function and energy requirements. Since the mean aerobic dive limit is about 44 s Tufted Duck diving to between 1–3 m for about 18 s are surfacing before their oxygen stores are exhausted (Halsey *et al.* 2003a; Woakes & Butler 1983). Although foraging captive Tufted Duck are resurfacing before the aerobic dive limit, the rate of oxygen uptake is greatest in the first 3 s of the surface period (Parkes *et al.* 2002). Carbon dioxide partial pressures may influence dive and surface times; an increased amount of CO_2 is unloaded in the last breaths before a dive, and hypercapnia rather than hypoxia is more often the limiting factor during dives (Halsey 2003a). The energy costs of diving are significant; oxygen consumption when diving is about 3.5 times resting consumption (Butler 2000).

Heat is lost through feathers, feet and by the ingestion of cold food. In the case of the Tufted Duck, not only is the preferred food, Zebra Mussels *Dreissena polymorpha*, at ambient temperature, which may approach freezing in cold conditions, but diving for the mussels causes a drop in body temperature in winter. Tufted Duck require about 1.8 kg of mussels per day (de Leeuw *et al.* 1999), and the abdominal temperature falls after seven dives to 5.5 m at 10°C (de Leeuw *et al.* 1998). In deeper water the air in the feathers is compressed, insulation decreases and the rate of heat loss increases (de Leeuw *et al.* 1999). Compared to surface conditions, when the bird is surrounded by air, thermal conductance increases by 4.8 times on submersion in water (de Vries & van Eerden 1995).

Studies of captive Tufted Duck have shown that the time spent on the surface is significantly longer when the birds are diving in water temperatures of 7–11°C than when feeding in waters of 20–23°C (Carbone *et al.* 1996). For captive Tufted Duck observed on an outdoor pond, the average duration of a dive was similarly found to be relatively short in winter compared with summer conditions (de Leeuw *et al.* 1999). Winter, with low water temperatures and limited food resources, is a critical period in the life of the Tufted Duck; daily energy requirements rise from 680 kJ/day above maintenance costs in summer to 1,080 kJ/day in winter (de Leeuw *et al.* 1999). The potential consequences of adverse conditions in late winter was evident in 1986, when 94.4% of 3,000–6,000 diving duck found dead on the upper Rhine in Switzerland were Pochard *Aythya farina* and Tufted Duck. In the same year, Tufted Duck mortality in the western part of the Dutch Wadden Sea was estimated at 14,600 birds; 82% of all losses. Mortality was attributed to a combination of very cold conditions in March and depleted food resources (Suter & van Erden 1992).

The difference in the dive to surface time ratios reported by Dewar (1924) compared with those for captive Tufted

Duck in captivity suggest that the proportion of the feeding bout spent underwater is 30% greater in the wild. If the rate of heat loss determined in the laboratory is applicable to natural conditions, the longer periods spent under water whilst feeding in the wild would likely incur cumulative heat loss. This suggests that there must be a trade off between increased energy intake, which requires increased foraging time, and the need to minimise heat loss by decreasing dive time and increasing surface time. Given the relative lack of information on the feeding behaviour of Tufted Duck in the wild, this study aims to provide further data on the dive and surface times for individuals over a winter season, and thus indicate whether the difference in behaviour reported for wild and captive birds is attributable to natural variation in the birds' activity patterns.

Methods

Study area

Observations were made at Westwood Great Pool, Wychavon, Worcestershire, UK (52°16'0"N, 2°10'34"W) in winter 2008/09. This 28 ha man-made lake, created in the 17th century, is about 3 m deep over much of its area. Tufted Duck occur at the site each winter (Emley 2000–2006). Twenty-two visits to study Tufted Duck feeding at the site were made from 6 November 2008 to 25 March 2009, with visit numbers 1–5 being made in November, 6–9 in December, 10–13 in January, 14–17 in February and 18–22 in March. Most visits were within five to seven days of each other. To minimise diurnal effects, the visits were made 2–3 h after sunrise on each occasion. Observations were made using a 22× telescope and binoculars from a hide mid-way along the east side of the lake, where about 90% of the water surface could be seen. On two of the 22 visits to the site (visit numbers 10 and 14), 90% of the surface of the lake was frozen and the birds were congregated on a small area of open water; diving activity was not recorded on these two days because the data would have been unreliable. Tufted Duck occurred across Westwood Great Pool during the other 20 visits, though their distribution was patchy because the birds associated in groups.

Water temperature was measured from a landing stage (25 m in length) at the beginning of each visit, using a thermocouple connected to a hand-held meter via a 9 m cable (Labfacility Model 2020). The thermocouple was cast into the lake to the full length of the cable to a point about 34 m from the shore and sank to the benthos. The reading was allowed to stabilise and the measurement repeated; duplicates were always within 0.2°C. The average of the two readings was recorded, rounded to the nearest °C.

Activity budgets

The birds' activities were recorded at the beginning of each visit by scanning the flock and recording the behaviour of each Tufted Duck present on the lake. Just one flock scan was made per visit as subsequent observations focussed on continuous monitoring of individuals (*i.e.* focal bird samples) to measure their dive and surface times. Four main behaviour categories were recorded: foraging (diving or surfacing), resting (floating motionless on the water or sleeping), preening and swimming. In each flock-scan, all birds in the flock were checked, working systematically from one side of the flock to the other using a telescope. The gender and activity of each Tufted Duck was recorded on first being sighted; ducks which entered the visual field from the direction already scanned were ignored (after Altman 1974). Previous observations had shown that most Tufted Duck dives were of 20–25 s duration, with surface times about half of that (I. Sutherland unpubl. data). Each telescopic field therefore was viewed for 15 s to improve the likelihood of detecting submerged Tufted Duck, which were recorded as feeding.

Diving activity

Dive and surface times were determined by recording the dive cycles for up to nine ducks of each sex during each visit, rather than following fewer individuals for longer periods, to ensure that the data were representative for the flock as a whole. The Tufted Duck were unmarked and most moved about on the surface of the lake. As for the scan samples, monitoring of the birds' diving activities commenced by first observing a bird at one end of the lake then sampling individuals thereafter by working systematically through the flock. Just one bird was monitored for each successive optical field of the telescope, which each viewed a fresh area of water, to keep pseudo-replication of data to a minimum. The time available for Tufted Duck to intermingle was minimised by targeting one sex only for each pass through the flock. Once the first traverse was completed a second was initiated for the other sex. The gender scanned first was alternated on successive visits to the site. The number of dive cycles and ducks monitored at each visit varied, depending on the distribution and behaviour of the birds on the lake.

On locating a foraging Tufted Duck, its feeding activity was followed for 5–10 dives, with the dive and surface times being recorded (focal bird scan; Altman 1974). The number of dives measured per Tufted Duck varied from as low as five (which provided dive and surface times for ducks feeding relatively close to others) to a maximum of 10 (to minimise bias towards a well-placed duck). If there was doubt about the identity of a surfacing duck (*i.e.* whether there had been a switch of individuals during a focal scan) the data for that dive cycle were abandoned. Effort was made to notice patterns or markings in the birds' plumage, to increase confidence that the same individual was being monitored for the duration of a focal scan. Sequential diving and surfacing events were recorded by dictation to a continuously running tape recorder (Sony TCM 200DV). The tape was rerun in play mode and the duration of the dive and surface times for each dive cycle were measured using a lapping stopwatch (Argo 10 10633).

The mean dive and surface times, and the ratio of the mean dive to surface times, were calculated for each of the Tufted Ducks monitored at each visit. These were used to calculate the average dive and surface times for each of the 20 visits with usable data, and the latter were then used to determine the average dive and surface times for the whole of the study period.

Data for males and females were treated separately. Mean dive and surface times were calculated ± s.d. in each case. Mean dive and surface times recorded for each visit throughout the study were used to test for any differences between the sexes in their dive patterns (*i.e.* in dive time, surface time and the dive to surface time ratio). Pearson product-moment correlation was used to test whether there was an association between water temperature and the mean dive and surface times recorded for each visit. The mean dive to surface time ratios recorded for males and females throughout the study were compared with the dive to surface time ratios reported from six published studies of captive Tufted Duck.

Results

The activity budget data indicated that 59.5% of the males and 59.9% of the females present at Westwood Great Pool were feeding at the start of each visit, and that a further 21.8–23.4% respectively were swimming (Fig. 1). On average, 34.9 (± 7.1) males and 22.9 (± 6.7) females were present at each visit over the study period. Observations made of 6–9 Tufted Duck of each sex during each visit yielded an average of 65.5 (± 14.0) male and 65.0 (± 14.7) female dive and surface times during each visit; the means for each visit were then calculated. The mean dive and surface times over the whole of the study period were 23.4 s (± 2.5 s) and 10.7 s (± 1.6 s) respectively for males, and 22.2 s (± 1.6 s) and 10.4 s (± 1.6 s) for females. For both sexes the overall mean dive times were significantly longer than the overall mean surface times (t_{38} = 19.1, P < 0.001 for males and t_{38} = 23.5, P < 0.001 for females). There was no significant difference between males

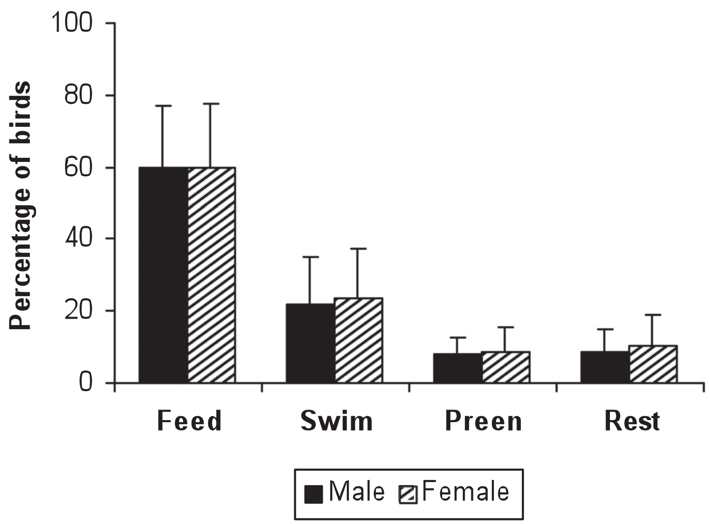

Figure 1. Tufted Duck activity (± s.d.) at Westwood Great Pool from November 2008–March 2009. Activity was determined once per visit (*n* = 20 visits with usable data) 2–3 h after sunrise.

and females in their mean dive times (t_{38} = 1.02, n.s.), nor in their mean surface times (t_{38} = 0.38, n.s.).

At each visit the mean dive to surface time ratio was close to 2 : 1 for both males and females (Appendix 1), with an overall mean dive to surface time ratio over the 20 visits of 2.3 : 1 (± 0.3) for males and 2.2 : 1 (± 0.3) for females. This is double the ratio calculated from ten experiments in six published studies of captive Tufted Duck feeding at depths of 1–3 m where the ratios of dive to surface time ranged from 0.8 : 1 – 1.4 : 1 (mean = 1.1 : 1 ± 0.2 : 1, Table 1). The mean dive to surface time ratios recorded for captive birds were all lower than the 2.2 : 1 ratio recorded for Tufted Duck in the wild and this difference was statistically significant (z_9 = 5.5 on comparing the ratio of 2.2 : 1 ± 0.3 recorded for wild birds with 1.1 : 1 ± 0.2 recorded for captive birds, P = 0.01).

Over the period November 2008–March 2009 the mean temperature at the benthos was 6.2°C (s.d. ± 1.6, range 4–8°C). There was no evidence for a correlation between water temperature and Tufted Duck feeding activity (*i.e.* their dive and surface times) within this temperature range (r_{18} = –0.37 and r_{18} = –0.18 for male dive and surface times; r_{18} = 0.01 and r_{18}= 0.05 for female dive and surface times; n.s. in each case).

Discussion

Activity scans recorded at Westwood Great Pool indicated that about 60% of both male

Table 1. Mean dive and surface times from six published studies of freely foraging captive Tufted Duck diving at 1–3 m.

	Depth of Dive (m)	**Dive Time, D** (s)	**Surface Time, S** (s)	**Water Temp** (°C)	**Ratio D : S** (X : 1)
Carbone (1996)	1.0	10.8	10.8	7–11	1.07
Carbone (1996)	1.0	11.8	12.0	20–23	0.98
Halsey (2003b)	1.1	11.2	12.3	10–18	0.91
Halsey (2003a)	1.3	13.3	13.1	15–18.5	1.02
de Leeuw (1998)	1.5	12.7	11.6	10.0	1.09
Woakes (1983)	1.7	14.4	16.1	13.6	0.89
Parkes (2002)	1.8	15.6	14.0	10–15	1.11
de Leeuw (1998)	2.5	16.4	19.8	10	0.83
Carbone (1996)	3.0	20.5	17.1	7–10	1.20
Carbone (1996)	3.0	20.9	15.2	20–23	1.38

and female Tufted Duck were feeding at the start of each observation period, and that a further 20% were swimming. These results are similar to those obtained at another lake about 5 km from the UK study site in 2001–2002 (I. Sutherland, unpubl. data), but differ from observations made on central European lakes where foraging was exclusively nocturnal (Pedroli 1982). Observations of the ducks' diving behaviour at Westwood Great Pool found that the dive time was significantly longer than the surface time for both sexes. Additionally, the mean dive to surface time ratio of 2.3 : 1 for males and 2.2 : 1 for females were both significantly greater than the mean dive to surface time ratios recorded for captive Tufted Duck in six laboratory-based studies (Carbone *et al.* 1996; Halsey *et al.* 2003a; Halsey *et al.* 2003b; de Leeuw *et al.* 1998; Parkes *et al.* 2002; Woakes & Butler 1993). The mean dive to surface time ratio was consistent and close to 2 : 1 for all 20 visits to Westwood Great Pool from November 2008 to March 2009. The present study therefore supports an earlier investigation into the foraging behaviour of Tufted Duck in the wild, which also found that the ratio of dive to surface times was about 2 : 1 (Dewar 1924).

Laboratory studies have indicated that in cold conditions the surface times of captive Tufted Duck increase and dive times decrease (Carbone *et al.* 1996; de Leeuw *et al.* 1999). Tufted Duck at Great Westwood Pool were foraging in water at a lower mean temperature than any of the captive groups, yet their mean dive and surface times of 23–22 s and 10–11 s gave dive to surface time ratios larger than in any of the studies in Table 1. Since wild Tufted Duck are diving with a surface time that is half of the dive time, they may be diving before complete re-saturation and taking advantage of the accelerated uptake of oxygen at low blood partial pressure (Carbone & Houston 1994). The foraging environment in the wild, which differs from that of captive Tufted Ducks who dive to trays stocked with food and who travel vertically, may also be influencing the results. In the wild, Tufted Ducks may have to search extensively on the benthos, all dives may not be successful, they frequently surface distant from the point of submergence and are exposed to cold and turbulent conditions. Other authors suggest that the difference between captive and wild Tufted Ducks in their dive to surface time ratios may be linked to captive Tufted Duck feeding without competition (Halsey *et al.* 2006), and have also questioned the usefulness of controlled laboratory experiments for predicting patterns of diving behaviour (Heath *et al.* 2007). Further investigation of Tufted Duck feeding activity in the wild would help to determine whether foraging behaviour varies over the entire diurnal period and how this compares with nocturnal foraging. Insight into the adaptability of Tufted Duck would be gained by examining their foraging behaviour in different environments and locations. There was no evidence for a correlation between water temperature and Tufted Duck feeding activity during the present study. The temperature range was quite narrow, however, and since dive depth is considered to be a strong determinant of dive time, variations in dive depth may mask any changes in dive time which are related to variations in water temperature.

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Appendix 1. Mean dive and surface times (± s.d.) recorded for Tufted Duck during each visit to Westwood Great Pool in winter 2008/09.

	Male			Female		
Visit	**Mean dive time (s) D**	**Mean surface time (s) S**	**Ratio D/S X:1**	**Mean dive time (s) D**	**Mean surface time (s) S**	**Ratio D/S X:1**
1	25.4 (2.6)	12.3 (1.1)	2.07	22.2 (1.1)	10.8 (2.0)	2.06
2	24.0 (4.3)	12.3 (2.9)	1.95	23.7 (2.7)	10.8 (1.6)	2.19
3	24.3 (6.9)	12.4 (3.4)	1.96	24.3 (2.9)	12.8 (2.7)	1.90
4	24.5 (4.7)	12.0 (2.7)	2.04	23.5 (3.1)	11.8 (2.3)	1.98
5	26.4 (3.4)	10.7 (2.3)	2.47	20.2 (2.6)	10.1 (1.1)	2.00
6	24.5 (3.5)	12.5 (3.0)	1.96	21.8 (3.1)	10.8 (2.9)	2.02
7	23.4 (2.4)	11.3 (4.1)	2.07	20.8 (4.2)	10.6 (2.5)	1.96
8	23.6 (2.3)	10.5 (1.8)	2.25	23.0 (3.4)	8.6 (2.2)	2.67
9	24.0 (2.5)	10.1 (3.5)	2.38	21.5 (3.0)	9.2 (2.1)	2.34
10	Frozen					
11	21.3 (3.5)	10.6 (1.7)	2.00	20.0 (2.3)	9.6 (2.8)	2.08
12	23.9 (4.3)	9.3 (0.9)	2.57	23.1 (1.4)	9.6 (1.8)	2.41
13	26.6 (4.0)	11.7 (1.9)	2.26	23.7 (2.5)	12.3 (1.9)	1.93
14	Frozen					
15	26.5 (4.9)	13.1 (3.1)	2.02	21.8 (1.7)	9.5 (0.8)	2.29
16	26.1 (2.8)	10.7 (3.0)	2.44	25.4 (2.4)	14.1 (2.8)	1.80
17	23.3 (2.4)	8.7 (1.5)	2.68	23.2 (3.2)	10.1 (3.7)	2.30
18	20.2 (3.8)	10.2 (2.1)	1.98	21.0 (5.4)	8.3 (3.9)	2.53
19	19.3 (0.9)	9.1 (3.4)	2.12	23.6 (1.6)	11.6 (3.2)	2.03
20	19.3 (4.9)	8.2 (3.2)	2.35	20.0 (3.7)	8.3 (3.2)	2.41
21	18.8 (5.5)	6.9 (2.9)	2.72	20.5 (2.9)	8.3 (2.1)	2.47
22	22.3 (3.8)	11.1 (3.1)	2.01	21.6 (3.6)	11.3 (2.3)	1.91

