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Short communication

Experiments on single diving birds in the laboratory often measure dives of decreased effort

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There have been a large number of laboratory experiments investigating the diving behaviour of Tufted Ducks *Aythya fuligula* (e.g. Butler & Woakes 1979, Woakes & Butler 1983, Houston & Carbone 1992, Halsey *et al*. 2005a). This species is common, hardy and adapts quickly to the laboratory environment. Thus, it is often the diving species of choice for testing hypotheses on the physiological and behavioural adaptations of divers to underwater foraging. To our knowledge, all previous investigations have studied birds diving alone, whereas in the wild Tufted Ducks are usually found in groups ranging in size from four or five birds to many hundreds. Therefore, under natural conditions they are usually competing with conspecifics for food. Because food is a finite resource, a Tufted Duck might be expected to attempt to maximize the proportion of the food that it ingests relative to that taken by conspecifics.

However, in the experimental dive tank, a solitary diving duck may recognize that it does not have to compete with others for the available food. This raises the question of to what degree the behaviour of a single bird while diving in a laboratory setting differs from that of many birds diving together. The most straightforward way to measure changes in diving behaviour is to record the time budget data of the dives (e.g. Houston & Carbone 1992, Halsey *et al*. 2005b). In the present study, the dive time budgets of Tufted Ducks diving alone or with conspecifics in a laboratory setting were measured to test whether diving behaviour differed under these two conditions. We hypothesized that Tufted Ducks diving in the dive tank with conspecifics would forage more intensively than Tufted Ducks diving in the dive tank alone. Furthermore, the diving behaviour of Tufted Ducks diving in the wild was observed to see whether the behaviour also differed in a natural setting between when diving alone and when diving with conspecifics.

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METHODS

Time budget data for Tufted Ducks were recorded in a natural setting on a large pond (inhabited by 10–15 Tufted Ducks) and in a laboratory setting (Home Office Licence No. PPL 40/1834) in a dive tank (five ducks) in the School of Biosciences, both at The University of Birmingham, UK. Data were recorded between January and March 2002 and April and May 2003, for both settings to avoid confounding effects of seasonality between conditions. The diving conditions in a dive tank and in the wild are inevitably somewhat different and thus direct comparisons of dive time budgeting between these settings would be difficult to interpret. Nevertheless, to enhance the value of comparing these two settings, in terms of the presence or absence of changes in diving behaviour when conspecifics are present, the depths of the dives between the natural and laboratory settings were matched as closely as possible. A map of the topography of the pond bed revealed that the water depth varied between 0.8 and 1.8 m; about 80% of the bed was between 1 and 1.2 m deep and less than 5% was greater than 1.5 m. Thus, the feeding tray suspended in the dive tank was positioned 1.1 m below the surface, encouraging the ducks in the laboratory to dive to this depth.

In the laboratory, birds were observed diving singly, in pairs or in threes. The birds were taken from an outside aviary where they had been reared and kept for several years. The aviary incorporated a pond where the birds dived for food thrown there. They then lived in the dive tank for a number of weeks before experiments started and quickly learnt to dive *ad libitum* for corn thrown onto the water. During experiments, diving behaviour was encouraged by adding maggots to the feeding tray. These birds had not previously been fed much live food and they seemed particularly motivated to dive for it; no training was therefore required to obtain foraging behaviour. To maximize the number of data points recorded for the birds in the laboratory setting when more than one bird was diving, the session was recorded onto videotape. The session could then be observed repeatedly so that the diving time budgets for each duck within the group could be recorded. For one bird and two birds together, dive duration, surface duration and the number of dives within each diving bout were recorded. We also measured descent duration, ascent duration, foraging duration (time spent at the feeding tray) and the percentage of the dive cycle (dive duration plus surface duration) spent foraging. Only the former set of values was recorded for three birds diving because of the difficulties in distinguishing between birds over very short periods of time.

To facilitate the recording of data at the pond, observers used binoculars and a stopwatch. The Tufted Duck chosen to watch was the first bird noticed to be diving. The number of conspecifics deemed to be within close proximity (about 5 m) of this bird was recorded. The subject bird was observed until it ceased diving (an observational session), and body markings (such as sex-specific plumage, tuft size

Table 1. Mean time budget data for five Tufted Ducks (n = 2031) diving in a dive tank. Values shown are mean ± se. In the upper part of the table, asterisks to the right of values indicate a significant difference between that mean value and the mean value directly below it. Asterisks to the left of values indicate a significant difference between the mean value for three ducks and the equivalent mean value for one duck. *$P < 0.05$, **$P < 0.01$.

	Dive duration (s)	Descent duration (s)	Foraging duration (s)	Ascent duration (s)	Surface duration (s)	Dive-to-pause ratio	Percentage of the dive cycle spent foraging	No. of dives per bout
One Duck	10.22 ± 1.21*	3.12 ± 0.55	4.86 ± 0.89*	2.22 ± 0.14	12.96 ± 1.77**	0.94 ± 0.13**	21.00 ± 0.03**	8.26 ± 0.70*
Two Ducks	12.18 ± 1.80	2.86 ± 0.30	6.57 ± 1.40	2.29 ± 0.17	10.29 ± 1.32*	1.32 ± 0.18*	28.38 ± 0.04	11.91 ± 1.49
Three Ducks	10.44 ± 0.73	–	–	–	**7.53 ± 0.82	**1.43 ± 0.14	–	9.98 ± 0.92

and any other specific markings) were noted and used to ensure that the same individual was being observed after each dive. Thus, only the diving behaviour of one bird could be recorded at a time. Dive duration, surface duration and the number of dives within each diving bout were recorded. Subsequent to the data collection, bouts of a duck diving were split into those in which the observed duck was deemed to have dived relatively far from other Tufted Ducks (no conspecifics within *c.* 5 m) and those in which the observed duck was diving in close proximity to a number of other ducks that were diving (one or more conspecifics within *c.* 5 m).

For both settings, subsequent to data collection, bout criterion interval analysis (Slater & Lester 1982) was used to eliminate all surface durations deemed to be interbout surface periods rather than interdive surface periods. Then the dive-to-pause ratio (a simple measure of diving effort in terms of the proportion of the dive cycle spent underwater) was calculated by dividing the dive duration by the surface duration.

The primary analysis testing for the effects on diving behaviour of the numbers of ducks diving, in the laboratory, employed paired *t*-tests. To avoid animal bias in the laboratory setting, mean values were obtained for each bird, which were used to obtain an overall mean. The secondary analysis testing for the effects, in the wild, of the number of birds diving on the diving behaviour of individuals employed Student's *t*-tests. All means are given ± se. Under the conditions of the natural setting, mean values for the behaviours observed from each session of observations were taken, from which an overall mean was calculated. This assumes that each session of observations was of a different Tufted Duck; however, given the limited number of ducks on the pond, the behaviour of some birds would have been measured during more than one observational session.

RESULTS

Data were collected in the dive tank for 2031 dives from five birds. On the pond, data were recorded for 1198 dives, for an estimated 10–15 Tufted Ducks. There were some significant differences in dive duration, foraging duration, the percentage of the dive cycle spent foraging and the number of dives per diving bout between one, two and three ducks diving in the dive tank. Each time the number of birds present in the tank increased, surface duration decreased significantly (by 42% between one and three Ducks diving) and the dive-to-pause ratio increased significantly (by 52% between one and three ducks diving; Table 1). There were no significant differences in any of the recorded dive time budget variables between one duck diving relatively close to or far from conspecifics on the large pond (Table 2).

DISCUSSION

In the dive tank, the dive time budgeting of Tufted Ducks changed with the number of conspecifics present and thus the hypothesis of the present study, that Tufted Ducks dive more intensively when with conspecifics, is accepted. Most apparent is the decrease in surface duration and increase in dive-to-pause ratio as the number of birds increased. This indicates a decrease in rest and an increase in diving effort as the number of conspecifics increases and is most probably explained by a resultant increase in competition for food.

That diving effort increases when more Tufted Ducks are present in the dive tank clearly shows that they are working less intensively when diving on their own. This lower work rate is probably the behavioural response of the ducks once they have learned that there is no competition for the food source. However, other explanations are possible for this lower diving effort, most notably a decrease in the time spent being vigilant at the surface for

Table 2. Mean time budget data for Tufted Ducks (n = 1198) diving on a large pond. Values shown are mean ± se.

	Dive duration (s)	Surface duration (s)	Dive-to-pause ratio	No. of dives per bout
One duck	18.30 ± 0.47	11.69 ± 0.70	1.85 ± 0.11	7.46 ± 0.81
Multiple ducks	17.39 ± 0.59	12.00 ± 0.78	1.75 ± 0.09	7.09 ± 0.66

a perceived threat of predation when conspecifics are present to share in this task (e.g. Roberts 1995).

Physiological adjustments to diving associated with diving behaviour (e.g. see Stephenson *et al.* 1986) might also differ between birds diving singly and those diving with conspecifics. This has important implications for the interpretation of data from experimental studies on Tufted Ducks and probably other species diving. For example, in a study to test quantifiably a foraging model for divers, which assumes that divers will forage optimally, Halsey *et al.* (2003b) recorded a mean (±se) surface duration in the control condition of 12.30 ± 1.42 s. This is very similar to that in the present study for one Tufted Duck diving in the dive tank. A crucial element of these models is the shape of the curve of cumulative oxygen uptake by the bird between dives, which is heavily affected by surface duration (Parkes *et al.* 2002, see also Halsey *et al.* 2003a). Our study indicated that the model did not quantifiably predict diving behaviour for individual ducks. However, given the large proportional differences in surface duration in the laboratory in the present study depending upon the number of birds present in the tank, the predictions of diving behaviour by the model would have been considerably different for birds diving with conspecifics. Furthermore, because the work rate of Tufted Ducks foraging in the presence of others is higher, they are probably foraging nearer to the optimal, and so this situation may have produced the diving behaviour predicted by the foraging model.

By contrast, the time budgeting of the ducks diving under natural conditions did not differ according to the proximity of conspecifics. This suggests that the perceived competition for food did not vary as it did in the laboratory setting. Tufted Ducks are gregarious and are rarely very far from conspecifics. Thus, even when they are the sole individual foraging at a particular patch, it is likely that they are aware that other Tufted Ducks could join them and start competing with them for the food resource. From this supposition, it would seem reasonable to expect Tufted Ducks to work more intensively when foraging regardless of the proximity of conspecifics present at the same foraging patch at any given moment. This lack of difference also suggests that vigilance against predators is not the explanation for the difference in diving effort observed in the laboratory setting, as clearly a perceived risk of predation will be at least as high in the pond setting and yet Tufted Ducks were not more vigilant when on their own.

Finally, the possibility that Tufted Ducks in fact dive co-operatively must also be considered in light of the results of the present study, as there is the prospect that the foraging of an individual may be facilitated by the prey capture of conspecifics as they sift through the mud. However, cases of truly co-operative feeding are only documented for some pelagic feeding birds (e.g. pelicans, Elliott 1992; penguins, Takahashi *et al.* 2004). Furthermore, as in the predator vigilance theory, if diving in groups facilitated prey capture, we would expect Tufted Ducks to change their diving behaviour on the pond in the presence of conspecifics, which was not the case. Thus, we conclude that competition seems the most likely explanation for the differences in diving behaviour between single and multiple birds in the laboratory setting.

It is usually accepted by experimenters that, for many reasons, the behaviour, and perhaps also the physiology, of birds diving in a laboratory setting cannot be translated to the wild in a simple manner. However, it is perhaps not often realized that birds diving alone in laboratory settings work less intensively than when diving with conspecifics. If a species under study competes with conspecifics when foraging in the wild, it is likely to be working more intensively there than when diving singly in the laboratory. Thus, the design of experimental protocols for the laboratory that make such subject birds compete for the food resource, or at least create the perception of competition, may facilitate the display of diving responses more akin to those that occur in natural settings.

REFERENCES

Butler, P.J. & Woakes, A.J. 1979. Changes in heart rate and respiratory frequency during natural behaviour of ducks, with particular reference to diving. *J. Exp. Biol.* **79**: 283–300.

Elliott, A. 1992. Family Pelecanidae (Pelicans). In Del Hoyo, J., Elliott, A. & Sargatal, J. (eds) *Handbook of the Birds of the World*, Vol. 1: 290–311. Barcelona: Lynx Edicions.

Halsey, L.G., Butler, P.J. & Woakes, A.J. 2005a. Breathing hypoxic gas affects the physiology as well as the diving behaviour of Tufted Ducks. *Physiol. Biochem. Zool.* **78**: 273–284.

Halsey, L.G., Reed, J.Z., Woakes, A. & Butler, P.J. 2003a. The influence of oxygen and carbon dioxide on diving behaviour of Tufted Ducks, *Aythya fuligula*. *Physiol. Biochem. Zool.* **76**: 436–446.

Halsey, L.G., Wallace, S.E., Woakes, A.J., Winkler, H. & Butler, P.J. 2005b. Tufted Ducks do not control buoyancy during diving. *J. Avian Biol.* **36**: 261–267.

Halsey, L.G., Woakes, A.J. & Butler, P.J. 2003b. Testing optimal foraging models for air-breathing divers. *Anim. Behav.* **65**: 641–653.

Houston, A.I. & Carbone, C. 1992. The optimal allocation of time during the diving cycle. *Behav. Ecol.* **3**: 255–265.

Parkes, R., Halsey, L.G., Woakes, A.J., Holder, R.L. & Butler, P.J. 2002. Oxygen uptake during post dive recovery in a diving bird *Aythya fuligula*: implications for optimal foraging models. *J. Exp. Biol.* **205**: 3945–3954.

Roberts, G. 1995. A real-time response of vigilance behaviour to changes in group size. *Anim. Behav.* **50**: 1371–1374.

Slater, P.J.B. & Lester, N.P. 1982. Minimising errors in splitting behaviour into bouts. *Behaviour* **79**: 153–161.

Stephenson, R., Butler, P.J. & Woakes, A.J. 1986. Diving behaviour and heart rate in Tufted Ducks (*Aythya fuligula*). *J. Exp. Biol.* **126**: 341–359.

Takahashi, A., Sato, K., Nako, Y., Dunn, M.J., Trathan, P.N. & Croxall, J.P. 2004. Penguin-mounted cameras glimpse underwater group behavior. *Proc. R. Soc. Lond. B.* **271**: 5281–5282.

Woakes, A.J. & Butler, P.J. 1983. Swimming and diving in Tufted Ducks, (*Aythya fuligula*), with particular reference to heart rate and gas exchange. *J. Exp. Biol.* **107**: 311–329.

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