Sex-specific dive characteristics in a sexually size dimorphic duck

SYLVIA K. OSTERRIEDER[1], MICHAEL A. WESTON[2]*, RANDALL W. ROBINSON[1] & PATRICK J. GUAY[1,3]

[1]Applied Ecology Research Group and Institute for Sustainability and Innovation, College of Engineering and Science, Victoria University – Footscray Park Campus, PO Box 14428, Melbourne MC, Victoria 8001, Australia.
[2]Centre for Integrative Ecology, School of Life and Environmental Sciences, Faculty of Science, Engineering and the Built Environment, Deakin University, 221 Burwood Highway, Burwood, Victoria 3125, Australia.
[3]Department of Zoology, University of Melbourne, Parkville, Victoria 3010, Australia.
* Correspondence author: E-mail: mweston@deakin.edu.au

Abstract

Dive duration generally increases with body size in animals including wildfowl. Therefore, diving behaviour may vary between the sexes in sexually size dimorphic species, such as the extremely sexually size dimorphic Musk Duck *Biziura lobata*. However, a previous study reports longer dives in the smaller sex (females) when breeding. In this study, non-breeding male Musk Ducks dived for significantly longer periods than females and tended to have longer inter-dive intervals, conforming to the general patterns described for other species. The differences in dive behaviour we describe may be explained by niche partitioning or differential oxygen requirements or uptake rates by the sexes.

Key words: *Biziura lobata*, diving physiology, Musk Duck, niche partitioning.

Dive duration is influenced by many factors, including extrinsic factors such as prey distribution, depth and climatic conditions, and intrinsic factors such as duration of preceding and subsequent inter-dive intervals (Sjöberg & Danell 1982; Stephenson *et al.* 1986; Kramer 1988; Beauchamp 1992; Halsey *et al.* 2006; Michot *et al.* 2006). Body size also influences dive duration and inter-dive interval. Due to the greater capacity of oxygen storage, larger animals are able to make deeper and longer dives (*e.g.* Beauchamp 1992; Boyd & Croxall 1996; Mori 2002), but stay at the surface for longer than smaller divers because the partial pressure between lungs and tissue is lower meaning oxygen uptake is slower (Mori 2002; Halsey *et al.* 2006). The relationship between body size and dive duration suggests that in sexually dimorphic species, the larger sex should have longer dives and inter-dive intervals due to their greater oxygen storage capacity.

Interestingly, the influence of sexual dimorphism on diving has not often been discussed. Differences in diving patterns between the sexes within size dimorphic species have been observed in marine mammals (*e.g.* Boyd & Croxall 1996; Page *et al.* 2005; Page *et al.* 2006; Staniland & Robinson 2008; McIntyre *et al.* 2010; Weise *et al.* 2010), penguins (Rey *et al.* 2013) and cormorants (*e.g.* Gómez Laich *et al.* 2012), but only rarely among highly size dimorphic wildfowl. We investigated dive and inter-dive interval durations between the sexes of an extreme sexually size dimorphic duck, the Musk Duck *Biziura lobata*. In particular, we wish to reconcile the prediction that the larger sex (males) will have longer dives and inter-dive intervals, with a previous report (McCracken 1999) of breeding members of the smaller sex having longer dives.

Methods

Musk Ducks forage mainly by diving to the bottom of lakes. Their diet differs between the sexes and consists of insects, their larvae and to a lesser extent molluscs, crustaceans, frogs and plant material (Marchant & Higgins 1990). Musk Ducks are extremely sexually size dimorphic with some males (1,700–3,100 g) being almost three times heavier than females (1,150–1,910 g) (McCracken *et al.* 2000). We conducted observations at the Western Treatment Plant (WTP; 38°00'S, 144°34'E), Victoria, Australia. Three ponds were used (115E-8, 115E-9, and 115E-10) for observations because of their heavy use by Musk Ducks (Loyn *et al.* 2002), their homogenous depth (2 m), temperatures and steep sides (see Halsey *et al.* 2006).

Observations

We conducted focal animal sampling on a haphazardly selected, mature ducks which could be unambiguously assigned a sex (n = 550; 7–10 min; total = 91.5 h), between March 2006 and February 2007. We divided the time of day into: morning (3.5 h after sunrise), mid-day (3.0 h around midday) and afternoon (3.5 h before sunset). Dive duration and inter-dive interval(s) were measured for each dive; observation bouts contained at least five consecutive dives and interbout intervals were excluded. Given the hundreds of ducks on the ponds (Guay 2008), and our efforts to avoid repeat-sampling, pseudo-replication is unlikely to be a major feature of our sampling.

Statistical analysis

We analysed the effects of sex, time of day and pond on dive duration and inter-dive interval using saturated linear mixed effects models (implemented in SPSS version 19) with each duck having a random intercept. Separate models were run for the dependent variables. In one model, dive duration was the dependant variable and preceding inter-dive interval duration was included as a covariate. In a second model, inter-dive interval was the dependant variable and the preceding dive duration was included as a covariate. Means are presented ± one s.d.

Results

A total of 608 dives were measured from 65 foraging ducks (36 females and 29 males). Dive duration was: males 35.2 ± 6.2 s and females 32.0 ± 5.4 s. Inter-dive intervals were: males 13.8 ± 5.6 s and females 11.5 ±

3.1 s. Males conducted 10% longer dives and 20% longer inter-dive intervals than females (Table 1). Dive duration also varied between ponds (115-P8: 35.4 ± 5.2 s, 115-P9: 31.2 ± 5.1 s, 115-P10: 34.0 ± 6.5 s) and was longer during the morning (34.5 ± 7.3 s) than other times of day (midday: 33.8 ± 5.8 s, afternoon: 32.3 ± 5.1 s); inter-dive interval was not influenced by time of day or pond (Table 1). Dive duration was not correlated with the preceding inter-dive interval nor was inter-dive interval correlated to the preceding dive duration (Table 1).

Discussion

Male Musk Ducks conducted significantly longer dives than females; similar but less pronounced patterns occur in some cormorants (Gómez Laich *et al.* 2012) and the opposite pattern was recorded among breeding Musk Duck (McCracken 1999). Breeding female Musk Ducks increase their body weight by > 20% before egg laying (Briggs 1988) and so may intensify their foraging effort by increasing their dive duration (McCracken 1999; Falk *et al.* 2000). The ducks we measured were not breeding, so breeding status could explain this discrepancy. The link reported here between sexual size dimorphism and diving behaviour can be explained by either differences in oxygen storage and uptake capacities (Kooyman 1989; but see Weise & Costa 2007), diet differentiation or niche partitioning between the sexes (*e.g.* Casaux *et al.* 2001; Ishikawa & Watanuki 2002; Beck *et al.* 2005; Cherel *et al.* 2007). Interestingly, differences in diet and foraging behaviour are reported for diving species exhibiting only small sexual size dimorphism (*e.g.*

Table 1. Results of the mixed model analyses. Influences of sex, time period, season, and pond on the dive duration ("Dive") and inter-dive intervals ("Inter-dive") of Musk Ducks as well as the variation by dive duration on the inter-dive interval and vice versa.

Term (subscript identifies the model)	*F*	d.f.	*P*
Sex_{Dive}	9.35	1, 58.7	**0.003**
$\text{Observer}_{\text{Dive}}$	0.06	1, 57.2	0.804
$\text{Time period}_{\text{Dive}}$	3.34	2, 58.0	**0.042**
$\text{Pond}_{\text{Dive}}$	5.31	2, 58.2	**0.008**
$\text{Inter-dive}_{\text{Dive}}$	3.26	1, 563.2	0.072
$\text{Sex}_{\text{Inter-dive}}$	4.73	1, 51.9	**0.034**
$\text{Observer}_{\text{Inter-dive}}$	0.69	1, 43.4	0.410
$\text{Time period}_{\text{Inter-dive}}$	1.42	2, 46.1	0.253
$\text{Pond}_{\text{Inter-dive}}$	6.38	2, 47.4	**0.004**
$\text{Dive duration}_{\text{Inter-dive}}$	1.36	1, 245.1	0.244

Lewis *et al.* 2002). Due to the extreme sexual size dimorphism, Musk Duck males have much larger mandibles than females, and the sexes exhibit preferences for certain dietary items (Gamble 1966; Frith *et al.* 1969; McCracken *et al.* 2000).

The mean dive durations we recorded for Musk Ducks were 103% longer and 37% shorter respectively than those reported for both sexes by McCracken (1999) and for a single non-breeding male by Sedgwick (1954). These differences can apparently be explained by depth differences (McCracken 1999, 0.2–2.0 m; Sedgwick 1954, ca 12.2 m) as dive duration is positively correlated with depth in diving ducks (*e.g.* Halsey *et al.* 2006). We observed increased dive duration, but not longer inter-dive intervals, during the morning (*contra* McCracken 1999). Increased diving effort in the morning may represent the need for food after a longer foraging break during the night (this species may not forage at night; Guay 2008) or perhaps be due to increased prey availability then. Diurnal variation in foraging behaviour is common in ducks, with many displaying foraging peaks at dawn and dusk (*e.g.* Green *et al.* 1999). The observed differences in dive duration and inter-dive intervals between ponds may reflect differences in prey availability (Folk 1971).

Studies in various species of diving ducks report a correlation between dive duration and the following inter-dive interval (*e.g.* Beauchamp 1992; Malhorta *et al.* 1996; Parkes *et al.* 2002). However, we found no such correlation for Musk Ducks, perhaps because Musk Ducks did not dive close to their aerobic limits at the WTP or used the inter-dive interval for other activities like scanning for predators or prey handling (see Hamilton & Taylor 2006).

In conclusion, this study indicates that Musk Duck conform to the general principle that the larger sex makes longer dives and inter-dive intervals. It also suggests that the previous report of the smaller sex having longer dives may be explained by the influence of breeding on female dive behaviour.

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Photograph: Male Musk Dusk (foreground) between dives, while another (background) rests, by Sylvia Osterrieder.

