Diving behaviour, dive cycles and aerobic dive limit in the platypus *Ornithorhynchus anatinus*☆

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Abstract

We investigated the diving behaviour, the time allocation of the dive cycle and the behavioural aerobic dive limit (ADL) of platypuses (*Ornithorhynchus anatinus*) living at a sub-alpine Tasmanian lake. Individual platypuses were equipped with combined data logger–transmitter packages measuring dive depth. Mean dive duration was 31.3 s with 72% of all dives lasting between 18 and 40 s. Mean surface duration was 10.1 s. Mean dive depth was 1.28 m with a maximum of 8.77 m. Platypuses performed up to 1600 dives per foraging trip with a mean of 75 dives per hour. ADL was estimated by consideration of post-dive surface intervals vs. dive durations. Only 15% of all dives were found to exceed the estimated ADL of 40 s, indicating mainly aerobic diving in the species. Foraging platypuses followed a model of optimised recovery time, the optimal breathing theory. Total bottom duration or total foraging duration per day is proposed as a useful indicator of foraging efficiency and hence habitat quality in the species.
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1. Introduction

The platypus can be described as an opportunistic carnivore (Faragher et al., 1979) and is known to spend approximately half of its active time foraging for benthic invertebrates by diving and bottom-searching in freshwater habitats around Australia (Grant, 1983, 1995). Foraging behaviour of the animal typically consists of continuous diving activity interrupted by short intervals on the water surface where food is masticated and swallowed (Burrell, 1927; Kruuk, 1993; Grant, 1995). Although there have been some previous investigations of platypus diving patterns (Grant and Carrick, 1978; Grant et al., 1992; Grigg et al., 1992; Serena, 1994; Gust and Handasyde, 1995; Otley et al., 2000), information on the diving behaviour of platypuses is still limited (Kruuk, 1993; McLeod, 1993; Benson, 1997) and relies mainly on observations made in captivity or by researchers engaged in other aspects of platypus biology (Evans et al., 1994; Manger and Pettigrew, 1995). The objective of this study was to elucidate diving behaviour of free-living platypuses in a lake system. Studies on platypuses in lake habitats are sparse. Most studies of the behaviour and ecology

of platypuses in the wild have involved populations occupying lowland river and stream systems on mainland Australia. Otley et al. (2000) investigated platypus activity in a sub-alpine lake system using radio-telemetry. The present study aimed to build on this, and elucidate diving behaviour of platypuses in the same lake system using time-depth recorders (TDR), a technique not previously used in any studies of platypus ecology. Detailed data on time allocation of platypus dive cycles are of particular interest because they shed light on diving strategies used by the species and allow conclusions on physiological factors affecting platypus diving and foraging behaviour. Such information enables comparison of diving strategies utilised by different semiaquatic mammals (Kramer, 1988). Studies on otters show that detailed information on diving and foraging behaviour can be useful in the assessment of foraging efficiency of diving species in different habitats (Kruuk et al., 1990; Kruuk and Moorhouse, 1991; Watt, 1992).

2. Materials and methods

2.1. Study site

Field experiments were carried out at Lake Lea (41°30′S, 146°50′E), a sub-alpine lake in north-western Tasmania. Lake Lea is shallow with an average depth of 2–3 m at full winter levels and contains at least three deep holes at over 10 m (Otley, 1996). It has a number of associated permanent and ephemeral streams, pools and wetlands and is surrounded by different terrestrial vegetation communities including buttongrass, moorland, rainforest, native grasslands, eucalypt forest, woodland scrub and alpine heath. Lake Lea has an elevation of 820 m and a surface area of approximately 142 ha with a catchment of 1480 ha and an estimated volume of 2.6 million cubic metres (Cutler, 1992).

2.2. Animal capture and measurement of diving activity

Diving activity was measured in 11 individual platypuses (5 adult males, mass: 2.14 ± 0.34 kg (S.D.), 6 adult females, mass: 1.49 ± 0.07 kg (S.D.)) between November 1998 and January 2000. Platypuses were captured following the methods outlined by Grant and Carrick (1974)
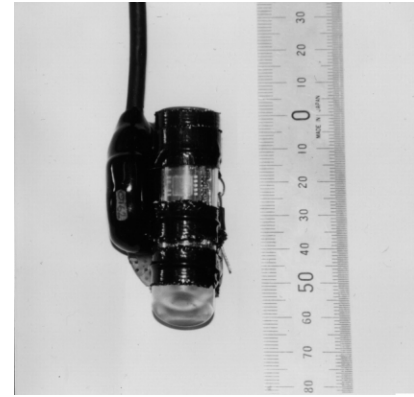

Fig. 1. Data logger–transmitter package used in this study.

and Serena (1994). Unweighted and partially weighted gill nets (50 and 15 m in length and 2 m in depth) were set in the lake and larger creeks and water bodies, while standard fyke nets with their distal ends staked several centimetres above water level were used in small creeks. Captured animals were marked with passive transponder tags (Trovan, Central Animal Records, Victoria) placed subcutaneously between the scapulae (Grant and Whittington, 1991). They were also weighed using a spring balance (Salter, Australia) and sexual status and age class were identified on the basis of spur and spur sheath morphology as well as body mass (Temple-Smith, 1973; Serena, 1994).

Individuals were equipped with combined data logger–transmitter packages (max $62 \times 28 \times 18$ mm^3, weight 50 g, Fig. 1) consisting of a specially designed standard transmitter (Faunatech, Eltham, Victoria) and a TDR (LTD_10, Lotek Inc., Canada). The packages were streamlined following the suggestions of Bannasch et al. (1994). They were attached with glue (5-min Araldite, Selleys Inc., Australia) to the guard fur of the lower back of the animals, just above the tail, following the method outlined by Serena (1994). Animals were then released at the site of capture. After approximately 2 weeks the animals were relocated by radio-telemetry using a portable radio-receiver (Wildlife Telemetry Inc.) and a three-element Yagi antenna. Animals were recaptured and the devices were removed by cutting through the fur underneath them. Animals were then weighed and measured before being released at the site of capture.

TDRs were of cylindrical shape with a drop nose to decrease drag (length 61.5 mm, $\varnothing$ 18 mm, weight in air 16 g). The devices allowed measurement of depth, ambient temperature and light levels with a data storage capability of 1 Mbyte (non-volatile FLASH memory). The depth range of the devices was 0–20 m. Pressure resolution was 0.06 psi equalling approximately 4 cm. Temperature range was from 2 to 25 °C with an accuracy of 0.06 °C. The devices were calibrated by the manufacturer (equipment for pressure-calibration: Superb-Barnet Pneumatic D/W Tester; for temperature-calibration: Neslab RTE-2000 Bath/Circulator and Omega HH40 Thermistor/Thermometer). The TDRs were programmed to measure dive depth in 2-s intervals and light intensity as well as ambient temperature in 2-min intervals. At these settings, recordings of up to 11 days were possible. After retrieval of the devices, data were downloaded with a specially designed reader and corresponding software (TAGTALK, Lotek Inc., Canada) to a laptop computer.

2.3. Data analysis

To analyse the dive data with respect to dive depth, dive duration, bottom duration, vertical speed and inter-dive surface duration, the software MULTITRACE 3.10 (Jensen Software Systems, Laboe/Germany) was used. Any excursion exceeding 0.15 m in depth was considered a dive. The end of a dive was defined as the time when the animal returned to the surface and reached a depth smaller than 5% of the maximum dive depth of the same dive. Vertical speed while diving was calculated by dividing dive depth by dive time needed to reach that depth. If vertical speed was less than 0.1 m s^{-1}, it was assumed that the platypus was at the beginning of a bottom phase; if vertical speed was greater than 0.1 m s^{-1}, this was assumed to represent the end of a bottom phase. Inter-dive surface duration was defined as the time span between two successive dives.

For further analysis, TDR data were averaged over 1-h observation intervals. Mean water and air temperatures were derived for each hour of foraging. Data were then analysed with respect to the number of dives performed per hour, mean dive duration, mean surface duration and mean dive depth. To account for repeated measures, statistical tests were made using single factor or multiway factorial analysis of variance. For multiple comparison, the Tukey test was used. To test for differences between two means, standard *t*-tests were performed. Simple linear regressions were calculated where appropriate. A probability of 95% ($P < 0.05$) was accepted as indicating statistical significance. Statistical testing was performed using SYSTAT.

3. Results

A total of 98 foraging trips (1095 h of foraging) from 11 platypuses (6 females, 5 males) were recorded during which 88 906 dives were performed. Dive duration, descent, bottom and ascent duration, surface duration and maximum dive depth were derived. Dive duration of platypuses at Lake Lea averaged 31.3 s (S.D.=4.0, $n=11$) with 72% of all dives ranging from 18 to 40 s (Fig. 2). Ninety-nine percent of all dives were less than 60 s. Maximum dive duration was 138 s. Bottom duration, i.e. the time platypuses spend close to the lake bottom searching for prey, averaged 21.3 s (S.D.=4.5, $n=11$). Mean surface duration between dives was 10.1 s (S.D.=2.0, $n=11$). Eighty-eight percent of all inter-dive surface durations lasted for less than 16 s. Mean dive depth was 1.28 m (S.D.=0.41, $n=11$) with a maximum of 8.77 m. Ninety-eight percent of all recorded dives were not deeper than 3 m.

Up to 1600 dives per foraging trip with a mean of 75 dives per hour (S.D.=9.14, $n=11$) were performed. Dive/surface duration ratios averaged 3.17 and 2.89, respectively, for summer and winter animals. Mean dive/surface duration ratio at Lake Lea was 3.10. Bottom/dive duration ratios averaged 0.74 for both summer and winter animals. A significant correlation between dive duration and dive depth was found (ANOVA, $P < 0.001$) and the relation is best described by the equation dive duration (s)$=30.17$ dive depth (m)$^{0.3001}$ ($r^2 = 0.96$). In addition, a low but significant correlation between dive duration and subsequent surface duration was observed (ANOVA, $P < 0.001$).

Mean dive duration, mean surface duration and mean dive depth was significantly different between the seasons (two-factor ANOVAs, $P < 0.05$ for any variable). Animals of both sexes dived significantly longer and deeper in winter than in summer (*t*-tests: $t = -2.469$, $P = 0.049$ and $t = -2.933$, $P = 0.017$, respectively). Also, surface duration was significantly longer in winter than that in summer (*t*-test: $t = -2.536$, $P = 0.032$).
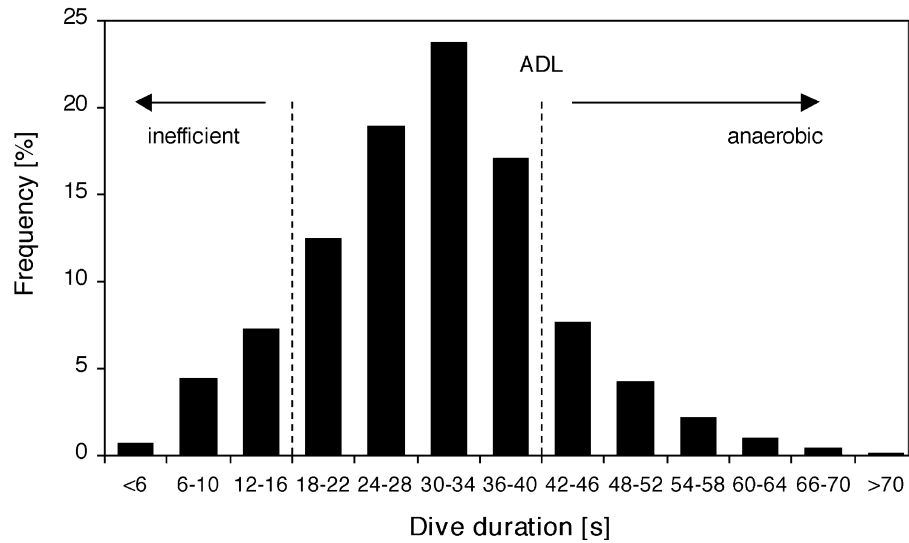
Fig. 2. Frequency diagram of platypus dive durations at Lake Lea ($n = 88\ 906$). Proposed behavioural ADL shown (40 s).

Correspondingly, mean dive duration (averaged over each hour) was significantly dependent on water and air temperatures with lower temperatures causing longer dive durations (ANOVA, $P = 0.001$ and $P < 0.001$ for water and air temperature, respectively).

Inter-dive surface durations of more than 1-min duration were defined as resting periods or breaks during foraging. Such a break in foraging activity occurred on average after every 25th dive. Overall, 61% of all breaks in foraging activity were between 1 and 3 min long. Only 1% of all breaks exceeded 10-min duration.

Foraging duration was defined as the time span between the beginning of the first dive and the end of the last dive of each foraging trip. Foraging duration averaged 11.5 h day^{-1} (S.D. $= 1.53$, $n = 11$) and was found to vary significantly according to season ($P = 0.041$) but not according to the sex of the platypuses ($P = 0.227$) (two-factor ANOVAs). Platypuses foraged for 12.2 and 11.2 h day^{-1} in winter and summer, respectively. Typically, platypuses began foraging immediately after leaving the burrow and foraged continuously over the whole duration of the foraging trip.

Mean deployment time for the packages was 31 days and ranged from 17 to 51 days (Table 1). Three animals dropped their packages. There was no significant difference between the mean mass of the animals before and after the deployment period (t-test, $t = 0.5$, $P > 0.3$). Recovery rate of data loggers was 100%.

Table 1
Details of animals used in field experiments

Sex	Capture date and time	Recapture date and time	Deployment duration (days)	Capture weight (kg)	Recapture weight (kg)
f	19.11.98 22:00	09.01.99 23:15	51	1.52	1.60
f	10.12.99 00:15	04.01.00 22:00	26	1.54	1.56
f	05.01.00 21:20	22.01.00 21:00	17	1.49	1.40
f	28.02.99 22:00	18.03.99 13:20	18	1.46	1.36
f	09.06.99 15:45	Logger dropped	Unknown	1.41	–
f	09.06.99 21:30	Logger dropped	Unknown	1.54	–
m	09.12.99 20:00	08.01.00 01:00	29	2.12	2.00
m	13.01.99 18:30	28.02.99 22:15	46	2.23	2.30
m	28.02.99 22:00	19.03.99 19:30	19	2.14	2.06
m	09.06.99 18:30	23.07.99 18:00	44	2.65	2.60
m	21.07.99 18:30	Logger dropped	Unknown	1.68	–

Table 2
Comparison of dive durations and surface durations recorded for platypuses

Mean dive duration (s)	Max. dive duration (min)	Surface duration (s)	No. of dives	Site/comment	Reference
30–60					Allport (1878)
120–180	10				Burrell (1927)
14	1			Captivity	Scheich et al. (1986)
	>6			Captivity	Jones et al. (1987)
34.8±11.9		12.7±6.9	437	Armidale, NSW	Kruuk (1993)
14–34	3.4	16–18	670	Duckmaloi Weir, NSW	McLeod (1993)
45–50				Broken River, QL	Lamm (1993)
28±1	11	73±5	488	Captivity	Evans et al. (1994)
30–60					Grant (1995)
20–40		10–20		Goulbourn River, Vic.	Gust and Handasyde (1995)
51.9/54.4		12.9/8.5	337/97	Bathurst, NSW	Benson (1997)
28.3–33.3		11.8–20.3	303	Lake Lea, Tasmania	Otley et al. (2000)
23.5±9.9	5		555	Captivity	Bethge et al. (2001)
31.3±4.0	2.3	10.1±2.0	88 906	Lake Lea, Tasmania	This study

4. Discussion

4.1. Instrumental and experimental effect

Several studies in the past have shown that externally attached devices can have important adverse effects on animals while swimming and diving. Effects range from increased foraging trip duration, reduced swimming speed and reduced food intake to increased energy expenditure and impaired movements (e.g. Wilson et al., 1986; Croll et al., 1991; Wilson and Culik, 1992; Hull, 1997). However, the data loggers used in this study did not cause a significant increase in the mean foraging metabolic rate of platypuses foraging in a swim tank (Bethge et al., 2001). This was most probably attributable to the streamlined shape of the devices, which is found to be most important for minimising instrument effect (Bannasch et al., 1994; Culik et al., 1994). The weight of the devices (50 g) amounted to only between 1.9 and 4.4% of body mass. Data loggers were attached to the lower back of the animals following the methods outlined by Serena (1994). In penguins, this was found to be the best position in order to minimise hydrodynamic drag of externally attached devices (Bannasch et al., 1994). However, adverse effects of the devices on the foraging behaviour of platypuses in their natural habitat cannot be ruled out. Platypuses at Lake Lea are considerably larger than animals from most other populations (Munks et al., 1996), which makes it easier to equip them with data loggers owing to their greater payload capacity. Increased care and the use of even smaller devices are indicated if experiments with data loggers are to be attempted on smaller individuals.

4.2. Platypus dive durations and the time allocation of the dive cycle

Foraging behaviour of platypuses in the wild consists of continuous diving activity interrupted by short intervals on the water surface where food is masticated and swallowed (Burrell, 1927; Kruuk, 1993; Grant, 1995). Reports on the duration of each single dive differ and range from an average of 14 s (Scheich et al., 1986) to an average of over 50 s (Benson, 1997). Most authors, however, report dive duration of between 20 and 60 s (e.g. 30–60 s, Allport, 1878; Grant, 1995; 34.8 s, Kruuk, 1993; 14–34 s, McLeod, 1993; 20–40 s, Gust and Handasyde, 1995). Results presented here are in line with these findings. Also, surface durations reported by other authors (Kruuk, 1993; Gust and Handasyde, 1995; Benson, 1997) are comparable to those found in this study (Table 2).

The relatively large variation of dive and surface durations of platypuses in the literature leads to the assumption that platypus diving behaviour must vary with some environmental variables. The results of this study suggest that the most important variable explaining differences in dive and surface durations of platypuses is water depth. In winter, water levels at Lake Lea were up to 60 cm higher than that in summer. Platypuses had to dive deeper in winter, which in turn increased dive durations

Table 3
Diving behaviour parameters of platypuses at Lake Lea in summer and winter

	Summer	Winter
Dive duration (s) (S.D.)	29.2 (5.4)	34.4 (2.5)
Bottom duration (s) (S.D.)	21.7 (5.6)	25.3 (2.2)
Surface interval (s) (S.D.)	9.2 (1.5)	11.9 (2.0)
Dive depth (m) (S.D.)	1.07 (0.2)	1.64 (0.4)
Vertical speed (m s^{-1}) (S.D.)	0.29 (0.09)	0.36 (0.1)
Dive cycle duration (s)	38.4	46.3
Bottom/dive duration ratio	0.74	0.74
Searching efficiency (bottom/dive cycle duration ratio)	0.57	0.55
Dive/surface duration ratio	3.17	2.89
Foraging duration (h day^{-1})	11.17	12.18
Total bottom duration (h day^{-1})	6.26	6.70

Ratios between bottom and dive durations as well as searching efficiency remain nearly constant regardless of season.

and possibly surface durations. This explains the observed dependency of dive and surface duration on season.

Mean dive depths of platypuses at Lake Lea in winter were elevated by about the same amount (on average 63 cm) as water levels, suggesting that platypuses chose to use the same foraging locations in both seasons and did not move to shallower areas. Maintaining the same foraging locations throughout the year, however, results in an increase in energetic costs associated with deeper diving in winter. Dunstone and O'Connor (1979) suggested that the time spent under water requires diving mammals to optimise search effort, including travel time to and from the surface, as well as prey pursuit time. In the case of the platypus, for a dive to be beneficial the energy content of the prey found during a dive must outweigh the energetic costs of travelling to and from the surface as well as of the searching behaviour on the bottom. Therefore, the success rate of each single dive is directly dependent on food quality and quantity in a particular area as well as on the duration of the search period, i.e. the bottom duration.

The techniques used in this study enabled for the first time the measurement of bottom duration (amount of time spent searching for prey) of platypuses in the wild. Although longer descent and ascent times prolonged dive durations in winter, bottom duration was also higher in winter than in summer (Table 3). Interestingly, the ratio between bottom and dive durations remained constant throughout the year (Table 3). In both summer and winter, 74% of the whole dive duration

was spent on the bottom of the lake during search behaviour. In addition, searching efficiency, defined as bottom duration divided by dive plus surface duration (Dolphin, 1988; Nolet et al., 1993), remained nearly constant regardless of season (Table 3). This indicates that although platypuses have to dive to greater depths in winter, the time the animals allocate for prey pursuit per time unit foraging remains constant. By extending the duration of each single dive cycle, animals make up for the disadvantages experienced through higher water levels.

The results of this study clearly show that platypuses follow the optimal breathing theory proposed by Kramer (1988) (see also Nolet et al., 1993; Houston and McNamara, 1994). It is based on the assumption that the diver maximises its long-term rate of energetic gain during foraging by optimising recovery time. Kramer (1988) argued that oxygen stores are replenished according to a curve of diminishing returns. The author assumed that the amount of oxygen remaining at the end of a dive cycle (dive duration plus surface duration) would be unaffected by dive depth. The theory predicts that both dive duration and surface duration should increase in dives at greater depths. If it is assumed that the time spent at the bottom is maximised, bottom duration should also increase with depth (Wilson and Wilson, 1988). This is exactly what was found for the platypus in this study.

Although searching efficiency (prey search time per unit foraging time, i.e. bottom duration divided by dive cycle duration) remains nearly constant throughout the year (Table 3), foraging efficiency

(i.e. foraging gain per unit effort) is likely to decrease in winter owing to a likely reduction in prey availability in the winter months (Faragher et al., 1979; Lamm, 1993; Otley, 1996) in combination with higher energetic costs due to lower temperatures (Grant and Dawson, 1978; Bethge et al., 2001). To maintain foraging efficiency, platypuses have to increase the time available for prey searching, i.e. the bottom time. It appears that platypuses at Lake Lea achieve this by extending the overall daily foraging duration during the winter months. Despite the fact that platypuses had to dive deeper during the winter, calculation of total bottom duration per day (by multiplying foraging duration with bottom/dive cycle duration ratio, see Table 3) yields a higher value for the winter months (6.70 h day^{-1}) than that for summer (6.26 h day^{-1}). Other mechanisms that might make up for the energetic disadvantages in winter are, for example, the utilisation of a larger variety of prey species as suggested by Faragher et al. (1979) or the shift to an energetically less demanding diurnal activity pattern.

Kruuk (1993) suggested that the ratio between dive and surface durations could be used as a measure of foraging efficiency in the platypus, a lower dive/surface duration ratio representing greater foraging efficiency. The results obtained in this study, however, indicate that this theory might be too simplistic. A lower mean dive/surface duration ratio (2.89) was found in the winter months at Lake Lea (Table 3). This was consistent with results obtained by Otley (1996) who calculated dive/surface duration ratios of 2.2, 2.87 and 3.2 for three platypuses foraging in Lake Lea in late winter. Following Kruuk (1993) this would imply higher prey densities in the cold season, which is highly unlikely (Faragher et al., 1979; Lamm, 1993; Otley et al., 2000). Kruuk (1993) argued that in a diving multi-prey loader like the platypus (in contrast to single prey loaders like otters) the time on the surface must be used to process captured prey during almost every surface interval. However, platypuses are known to store considerable amounts of prey in their cheek pouches (Grant, 1995). This could well be an adaptation to actually avoid the need for lengthy food processing during active foraging in order to maximise bottom time and therefore foraging efficiency. Platypuses are more likely to follow a foraging strategy where food processing is mainly undertaken during prolonged resting periods either in the burrow or on the water surface. Analysis of dive profiles showed that resting periods of more than 1-min duration occurred on average after every 25th dive, which seems to be a reasonable number to fill the cheek pouches.

Dive/surface duration ratio does not seem to be a useful measure to compare foraging efficiency of platypuses between different habitats. Instead, ideally total bottom duration or, if not available, total foraging duration per day might be a better measure of foraging success and an indication of habitat quality. Captive studies suggest that platypuses will not spend more time than necessary in the water (Bethge et al., 2001; Krueger et al., 1992; Hawkins and Fanning, 1992; Grant, 1983). Also, this study suggests that the time budget of the platypus' dive cycle is rather static and is influenced by a number of environmental factors including depth and water temperature, which are mainly beyond control of the animal. Therefore, the only possibility of increasing foraging success is to increase foraging duration in order to maximise bottom duration. Consequently, habitat quality may be assessed by measurement of platypus bottom durations with longer total bottom duration suggesting a less productive environment.

4.3. Maximum dive times

Platypuses are able to spend extended periods of time inactive under the water surface ('wedging') (Scheich et al., 1986), during which time their metabolic rate is very low (Bethge et al., 2001). However, reports on 'wedging' duration (maximum dive times) differ in the literature (Table 2) and most observations were made in captivity rather than in the wild. Out of more than 88 000 dives performed by the 11 eleven animals observed at Lake Lea over several days (each for more than 1100 h of foraging), only 10 dives were longer than 80 s with a maximum dive duration of 138 s. This suggests that inactive diving in platypuses in the wild is much more limited than previously thought. Johansen et al. (1966) questioned the long dive times estimated by earlier authors and reported dive times of approximately 3 min to be close to the endurance limit of the animal. McLeod (1993) reported maximum dive times of 140 s for platypuses foraging in the Duckmaloi Weir, NSW. The longer 'wedging' periods of platypuses observed by Jones et al. (1987), Evans et al. (1994) and Bethge et al. (2001) are
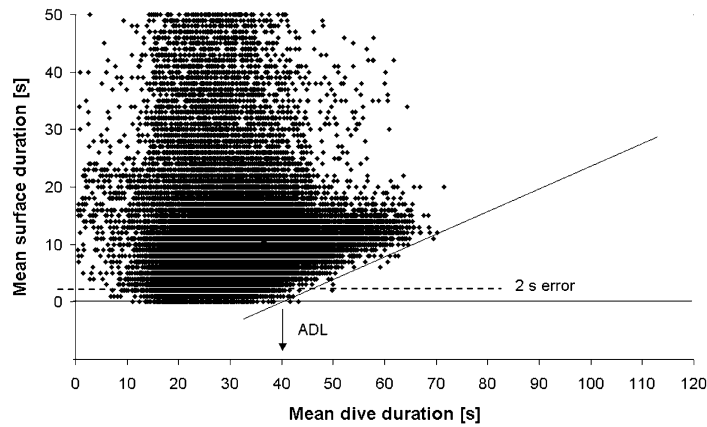
Fig. 3. Mean surface duration of three successive dives of platypuses at Lake Lea ($n = 88\,906$) plotted against mean dive duration of the same dives. Values under 2-s surface duration are inappropriate due to data logger sampling rate. Solid line describes minimal surface duration. Arrow shows proposed behavioural ADL (40 s).

likely to be typical for animals in captivity where possibilities for hiding are limited. This study suggests that in emergency situations in the wild the platypuses would rather try to find a hiding position in shallow water under e.g. overhanging vegetation or roots where they still have access to air. This would avoid risky situations where they have to get to the water surface owing to oxygen depletion. Accordingly, Otley and Munks (personal communication) observed platypuses resting inactive under ice close to breathing holes where they were able to stick their bill up to occasionally take a breath.

4.4. Aerobic dive limit

Foraging strategies of amphibious mammals are highly dependent on the animals' ability to stay submerged as time under water is directly related to foraging success (Dunstone and O'Connor, 1979; Kramer, 1988). The platypus resembles small eutherians and most diving birds in diving after inspiration (Evans et al., 1994). Oxygen can be stored in the lungs, in the blood and in the tissues of the animal and can then be made available during diving. The amount of oxygen stored and the energy consumption under water determine the time the animal can remain under water before oxygen stores are fully utilised, i.e. the aerobic dive limit (ADL) (Butler and Jones, 1997). If the ADL is exceeded, anaerobic metabolism begins to take over and metabolic end products, such as lactic acid, accumulate. In con-

sequence, the animal would have to spend a long time at the surface between dives to eliminate waste products from the body (Johansen et al., 1966; Butler and Jones, 1982).

The behavioural ADL of platypuses can be estimated using dive durations and surface durations obtained from the field experiments. Horning (1992) suggested that consideration of the surface interval vs. dive duration could yield an estimation for the behavioural ADL. However, simple inspection of post-dive surface intervals is problematic since platypuses may redive despite carrying an increased lactate load. The consideration of the surface interval vs. dive duration over a number of consecutive dives, however, can minimise this error (Horning, 1992). For the platypus, we regressed the mean post-dive surface duration of three successive dives against the mean dive duration of the same dives (Fig. 3). This was the minimum number of dives to obtain a relationship between minimal surface duration and dive duration (see for comparison Horning, 1992; Pütz, 1994; Bethge et al., 1997). Regression of minimal surface duration against dive duration (for dive durations with minimal post-dive surface durations of more than 2 s) yields the function minimal surface duration (s) = 0.37 dive duration (s) − 14.9 ($r^2 = 0.91$, $n = 12$, Fig. 3, solid line). The intersection of this function is an estimate for behavioural ADL and was 40 s. Dives lasting longer always had an increased surface duration, probably caused by a lactate load that had to be removed.

The distribution of dive durations in the wild (Fig. 2) suggests that an ADL of 40 s is likely for the platypus. Seventy-two percent of all dives in the wild ranged between 18 and 40 s. Only 13% of all dives performed were shorter. Only 15% of all dives derived from TDR exceeded the estimated behavioural ADL of 40 s (Fig. 2). To optimise time spent under water, i.e. foraging success, platypuses would do better to use all available oxygen stores in most dives rather than surfacing before oxygen stores are depleted (Wilson, personal communication). Indeed, swim tank experiments indicate that short dives are inefficient for the platypus (Bethge et al., 2001). On the other hand, depleting oxygen stores and consequently using anaerobic metabolism result in longer times at the surface between dives. Reduced foraging success is the consequence.

The low percentage of dives exceeding the behavioural ADL suggests that there is little need for anaerobic metabolism during normal diving behaviour in the platypus. This is consistent with the observation that platypus skeletal muscles have a low acid buffering capacity relative to other diving mammals (Evans et al., 1994; Jones et al., 1987). The use of mainly aerobic metabolism is also supported by the foraging behaviour of the platypus. Diving is closely associated with feeding habits and only occasionally with the animal temporarily seeking refuge. The platypus feeds in shallow water by diving for a mean of 31.3 s (this study), then returning to the surface for a mean recovery period of 10.1 s (this study) to masticate the food, whereafter the cycle is repeated. Such a pattern of behaviour seems best supported physiologically by rapid recovery between short dives in close succession to maximise the time spent under water searching for food. Short recovery times after dives suggest that there is little anaerobic metabolism (Evans et al., 1994). The ability to sustain prolonged submersion is only needed during emergency when anaerobic metabolism might take over.

5. Summary

Consistent with results on their energetic demands (Bethge et al., 2001), platypuses were found to forage close to their physiological limits in the wild following a model of optimised recovery time, the optimal breathing theory, proposed by Kramer (1988). In the platypus, the energy gained from a dive is proportional to bottom duration and the results of this study indicate that dive cycles are clearly organised so as to maximise bottom time. Searching efficiency remained constant regardless of water depth and season. Dive durations as well as surface durations consequently increased with dive depth, which was found to be the main factor influencing dive cycle time allocation. Accordingly, at Lake Lea longer dive durations were mainly observed in winter when higher water levels occurred. Due to higher metabolic costs and longer dive durations, ADL is exceeded more frequently during the cold season. To cope with the increased metabolic demands in winter, foraging duration is extended. Total bottom duration is proposed as a useful indicator of foraging efficiency in this species or, if this information is unavailable, foraging duration per day could be used.

The platypus is mainly an aerobic diver with the ability to forage for up to 40 s before oxygen stores are depleted. Mean dive durations of platypuses were considerably longer than those of semiaquatic eutherians. Kruuk (1993) suggested a correlation between log body mass and log mean dive duration in diving mammals and predicted a mean dive duration of only 13 s for the platypus. The unexpected long dive durations of platypuses presented here can be explained by the animals' low energetic costs for diving (Bethge et al., 2001) and consequently the relatively high ADL. However, maximum dive times of platypuses are likely to be shorter than previously reported.

with the fieldwork and to Mr H. Burrows for access to private land.

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