

**Energetics and foraging
behaviour of the Platypus
*Ornithorhynchus anatinus***

by

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requirements for the Degree of
Doctor of Philosophy

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Declaration of originality

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*For Tom, Louise, Karl, Albert, Eric,
Fritz, Gerda, Hilde,
Isolde, Julia, Konrad, Lydia*

Abstract

In this work, behavioural field studies and metabolic studies in the laboratory were conducted to elucidate the extent of adaptation of the platypus *Ornithorhynchus anatinus* to its highly specialised semiaquatic lifestyle. Energy requirements of platypuses foraging, resting and walking were measured in a swim tank and on a conventional treadmill using flow-through respirometry. Foraging behaviour and activity pattern of platypuses in the wild were investigated at a sub-alpine Tasmanian lake where individuals were equipped with combined data-logger-transmitter packages measuring foraging activity or dive depth and ambient temperature.

Energy requirements while foraging in the laboratory were found to depend on water temperature, body mass and dive duration and averaged 8.48 W kg^{-1} . Mean rate for subsurface swimming was 6.71 W kg^{-1} . Minimum cost of transport for subsurface swimming platypuses was $1.85 \text{ J N}^{-1}\text{m}^{-1}$ at a speed of 0.4 m s^{-1} . The metabolic rate of platypuses resting on the water surface was 3.91 W kg^{-1} while minimal RMR on land was 2.08 W kg^{-1} . The metabolic rate for walking was 8.80 and 10.56 W kg^{-1} at speeds of 0.2 and 0.3 m s^{-1} , respectively. Minimal cost of transport for walking was predicted to be $2.13 \text{ J N}^{-1}\text{m}^{-1}$ at a speed of 1.7 m s^{-1} . A formula was derived, which allows prediction of power requirements of platypuses in the wild from measurements of body mass, dive duration and water temperature.

Activity patterns of platypuses in the wild were highly variable. Forty percent of the platypuses studied showed patterns, which deviated considerably from the nocturnal pattern generally reported for the species. Some animals showed diurnal rhythms while others temporarily followed the lunar cycle. Foraging trips lasted for an average of 12.4 h of continuous foraging activity per day (maximum: 29.8 hours). There were significant differences in diving behaviour between sexes and seasons. Activity levels were highest between August and November and lowest in January.

While foraging, platypuses followed a model of optimised recovery time, the optimal breathing theory. Mean dive duration was 31.3 seconds with 72%

of all dives lasting between 18 and 40 seconds. Mean surface duration was 10.1 seconds. Mean dive depth was 1.28 m with a maximum of 8.77 m. Up to 1600 dives per foraging trip with a mean of 75 dives per hour were performed. Only 15 % of all dives were found to exceed the estimated aerobic dive limit of 40 seconds indicating mainly aerobic diving in the species. Total bottom duration per day was proposed as a useful indicator of foraging efficiency and hence habitat quality in the species.

In contrast to observations made earlier in rivers, temporal separation was found to play a vital role for social organisation of platypuses in the lake system that was investigated. It is suggested that high intra-specific competition as well as limited burrow sites and a limited number of at the same time highly productive foraging locations were responsible for this observation. Mean burrow temperature in the wild was 17.5 and 14.2°C in summer and winter, respectively, and was fairly constant over the platypus's resting period. In the cooler months, burrow temperature was up to 18°C higher than ambient air temperature.

By combining both field and laboratory data, a time-energy budget for the platypus was created. Mean field metabolic rate was 684 kJ kg⁻¹ day⁻¹ and was significantly higher in the winter months. Mean food requirement was 132 g fresh matter kg⁻¹ day⁻¹. Feeding rates were 68 % higher in winter than in summer.

While platypuses in the swim tank were found to expend energy at only half the rate of semiaquatic eutherians of comparable body size, cost of transport at optimal speed as well as field metabolic rates were in line with findings for eutherians. These patterns suggest that locomotor efficiency of semiaquatic mammals might have reached a limit for energetic optimisation. The semiaquatic lifestyle seems to pose comparable energetic hurdles for mammals regardless of their phylogenetic origin.

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1 **General introduction and aims**

Research on diving animals has concentrated mainly on aquatic species in the past. Studies on the energetics of such species have revealed specialised physiological adaptations and surprisingly low costs for under water locomotion, mainly explained by highly adapted swimming modes and body morphologies (Bannasch 1995, Kooyman and Ponganis 1998, Williams 1998). Studies of semiaquatic animals, however, which use paddling modes for propulsion, have revealed higher energy costs for swimming than specialised divers as determined from measurement of oxygen consumption (Fish 1982, Williams 1983a, Baudinette and Gill 1985, Williams 1989). The intermediate lifestyle between two media requires a compromise in morphological adaptations resulting in increased energetic demands (Williams 1998).

The platypus *Ornithorhynchus anatinus* is the only prototherian mammal living today that has adopted a semiaquatic lifestyle. Its position between terrestrial and aquatic specialists suggests that it will have high energy requirements for locomotion (Fish and Baudinette 1999) and these may be further increased by thermoregulatory constraints due to its relatively low body mass (Hind and Gurney 1997). Throughout its distribution the species occupies a wide range of climatic conditions, from tropical to cool temperate including sub-alpine mountain and alpine tableland areas where, in winter, it may be exposed to air temperatures well below freezing and water temperatures approaching 0°C. This makes it evident that the species has the capacity to cope with severe environmental stresses despite possible energetic constraints.

The platypus is common in the lakes, rivers and streams of eastern and southeastern Australia from the Cooktown area in the north to Tasmania in the south. Individuals have been found in shallow creeks, irrigation trenches, muddy lowland rivers, highland lakes and large rapidly flowing rivers, man-made impoundments, backwaters and wetlands as well as estuarine habitats and even polluted streams in metropolitan areas (Grant 1983a, Hird 1993, Serena et al. 1998). The ideal habitat of the platypus is a slow flowing river or stream with relatively steep earth banks consolidated by the roots of native

plant species whose foliage overhangs the banks (Grant and Temple-Smith 1998). The river or stream itself has a diversity of benthic substrates including logs and snags, and a diversity of aquatic vegetation (Rohweder 1992, Bryant 1993). Ideally, the habitat consists of a series of distinct pools separated by riffle areas. It is characterised by a bed with either rocky substrata or with a heavy silt or branch covering, water depths of around two metres, and heavily shaded by overhanging vegetation (e.g. Benson 1997, Bryant 1993), which provides organic materials for benthic invertebrate diversity.

The platypus appears to have overcome the constraints of its semiaquatic lifestyle, in part, by a combination of morphological and physiological strategies. Despite early reports to the contrary (Martin 1902, Smyth 1973), it is well able to maintain its body temperature of 32.1°C even under harsh winter conditions (Grant and Dawson 1978a). The platypus is known to be able to spend long periods continuously foraging in water at nearly 0°C (Grant and Dawson 1978a, Grant and Dawson 1978b). It does this by utilising many of the physiological adaptations seen in other amphibious mammals (Irving 1973) such as maintenance of a constant body temperature by an increase in metabolic activity, the possession of a vascular counter-current heat exchange system at the base of the hind legs and tail and a low conductance (high insulation) of both tissue and fur. Platypus fur consists of a thick mass of short woolly underfur with kinked fibres to facilitate the holding of a layer of still air next to the body, overlain by less numerous primary or guard hairs (Grant and Dawson 1978a). Guard hairs add to the ability of the fur to trap an air layer during immersion in water. Estimates of the density of platypus fur range between 600 to 900 fibres per mm² (Carter 1965, Grant and Dawson 1978a). The occupancy of burrows and the curled sleeping posture adopted by the platypus are probably also very efficient in helping to conserve body heat (Grant and Dawson 1978a). On the other hand, platypuses are known to be intolerant of temperatures higher than 25°C because they lack any means of evaporative cooling. This factor might be involved in their limited distribution in the tropical north of Australia (Grant and Temple-Smith 1998).

Studies into the diet of platypuses have shown that their prey almost exclusively consists of benthic invertebrates, mainly insect larvae (*Trichoptera* and *Ephemeroptera*), with relatively little variation between the areas studied (Grant and Carrick 1978, Faragher et al. 1979, Grant 1983). The presence of free-swimming species such as shrimp, crayfish, beetles, water bugs and tadpoles in the platypus's diet has also been reported (Burrell 1927, Fleay 1944, Faragher et al. 1979). During foraging, the platypus's bill rakes through and along the substrate, with lateral movements of two to three times per second while prey is detected using electro-location (Scheich et al. 1986). It has large webs extending well beyond the toenails, a broad, flat tail and swims by paddling with its forelegs in alternating strokes, its hind legs and tail trailing behind.

Platypuses are seasonal breeders, with both spermatogenesis and the size of the venom-secreting male crural glands reaching a maximum from August to October (Temple-Smith 1973). Breeding season appears to vary with latitude and climate (Griffiths 1978, Grant 1989). Platypuses are thought to engage in a polygynous mating system and it is proposed that a system of dominance or hierarchy is established (Temple-Smith 1973, Grant 1983a, Grant and Temple-Smith 1998). During the breeding season, spatial separation has been reported, when animals occupied separate core areas (Serena 1994, Gust and Handasyde 1995).

The main objectives of this current study were to investigate the behavioural ecology of free-living platypuses in a sub-alpine lake system, to clarify the degree of physiological and behavioural adaptation achieved by the species and to present a time-energy budget for the animal. To meet these objectives, platypus energetics during aquatic and terrestrial locomotion were examined in a captive study using respirometry. Secondly, a field study was conducted to investigate foraging behaviour in the wild. Metabolic rates derived in the laboratory and behavioural data from the field were combined to calculate seasonal energy demands for the species. Costa (1988) noted that time-energy budgets were a fruitful area of study and that, if behavioural data are collected

concurrently with measurements of energy expenditure, one may begin to create a time-energy budget for the freely diving animal. The current study aimed to test the feasibility of this method in a semiaquatic species like the platypus and to compare the method with other approaches used to investigate the energetic demands of free-living animals.

The field studies focused on a population inhabiting Lake Lea, a sub-alpine lake in northwest Tasmania. A lake was chosen since most of the studies to date on the diving behaviour and foraging ecology of platypus have concentrated on populations inhabiting river systems. Also, platypuses are particularly abundant in Lake Lea and they appear to be free of the fungal disease, which has been found in some lowland populations in Tasmania (Obendorf et al. 1993). Investigation of platypus activity pattern in a sub-alpine habitat is also of interest in respect to the thermoregulatory ability of the species. The occurrence of the species in cold habitats is quite common. In Tasmania, they have been sighted in Lake Dobson (1025 m), Lake Newdegate (1138 m) and Lake Wilkes (1100 m) in Cradle Mountain National Park. On the mainland, platypuses have been investigated in the Thredbo River at Jindabyne (920 m) (Grigg et al. 1992). However, the question of torpor or hibernation is still not conclusively answered for the species and it is tempting to speculate about possible seasonal changes in activity pattern due to harsh climate conditions.

This study also aimed to elucidate in detail the diving behaviour and the foraging pattern of platypuses in the wild. Because of recent advances in the field of microelectronics, archival tags (data-loggers) could be used, which allow the measurement of diving and foraging parameters in excellent time resolution. Platypus activity patterns have been studied previously by a number of authors (e.g. Kruuk 1993, McLeod 1993, Benson 1997). Platypuses are known to dive repeatedly during foraging, spending short periods between dives on the surface while masticating food. Recent studies have revealed predominantly nocturnal activity, with daytime activity occurring only in a number of cases (Serena 1994, Grant and Temple-Smith 1998, Otley 2001). However, the methodology of studies into activity pattern of platypuses have been

limited so far to radio-tracking techniques or direct observations only. Reports on the duration of active periods in platypuses for example differ considerably in the literature and range from 7 to 19 hours.

Information on the metabolic needs of platypuses is still sparse and in part contradictory. Fish et al. (1997) for example reported active metabolic rates for the platypus which were lower than resting metabolic rates reported earlier by Grant and Dawson (1978a). While early authors described the animals' swimming mode as fundamentally inefficient (Howell 1937) recent work attributed the platypus with highly developed adaptations for diving (Grant and Dawson 1978a, Fish et al. 1997). Further investigation of the energetics of platypus locomotion is indicated, especially in view of its monotreme origin. A comparison of the platypus' energy demands and its adaptations to swimming and walking with those of semiaquatic eutherians should provide further information on the energetics of the monotremes, and thus on the evolution of endothermy in mammals.

The status of the platypus has been described as common but vulnerable (Carrick 1983). Platypuses are reputed to have declined sharply in numbers during the days of trade in their furs, before their protection in all states in 1912 (Burrell 1927, Grant and Temple-Smith 1998). Today, data from netting and observations indicate a reduction in local distribution and numbers of platypuses due to human activities. Grant and Temple-Smith (1998) suggested that continued and increased disturbance of habitat caused by poor land management practices, such as farming and forestry, have resulted in population declines. Overall it can be seen that there is a need for research, in particular in the area of habitat requirements, so that effective management plans can be developed.

Part of this work has been published in the Journal of Comparative Physiology B (Bethge et al. 2001). Results from the field work experiments are currently prepared for publication. Preliminary results have been published in the proceedings of the 1999 Tasmanian Platypus Workshop in May 1999 in Hobart, Tasmania (Bethge et al. 2000a, Bethge et al. 2000b). Also, data on metabolic rates, activity levels and diving behaviour has been presented on the 15th Annual Meeting of the ANZSCP in December 1998 in Perth, WA, and on the Australian Mammal Society Conference 1999 in Hawkesbury, NSW.

The field work of this thesis is part of a larger study into the ecology of platypuses at a sub-alpine lake in Tasmania in collaboration with Dr. Sarah Munks and Helen Otley (B.Sc.), School of Zoology, University of Tasmania, and Assoc. Prof. Stewart Nicol, Discipline of Anatomy and Physiology, School of Medicine, University of Tasmania. Results of this study have been published recently or are prepared for publication (Otley 1996, Otley et al. 2000, Munks et al. 2000, Munks et al. in prep.).

2 Study areas, animal details and general field methods

2.1 Study Areas

2.1.1 Salmon Ponds / Plenty River, southeast Tasmania

Platypuses for the laboratory experiments (Chapter 4 & 5) were captured in the Plenty River and tributaries at Salmon Ponds, Tasmania (42°45' S, 146°58' E, elevation 20 m; Photo 2-1, Fig. 2-1). The area is known to have a large population of platypus. The Inland Fisheries Commission operates a trout hatchery at Salmon Ponds adjacent to the Plenty River. A series of wide cement lined channels run through two large ponds where fish are kept for public display. Platypuses are regularly seen in the ponds and channels of the hatchery. There are distinct runways, which the platypus uses to leave or enter the river. Taylor et al. (1991) suggested that Salmon Ponds is attractive for the platypus because of oligochaete tubifex worms, which can be extremely abundant in the channels and ponds.



Photo 2-1: Plenty River, Salmon Ponds, southeast Tasmania

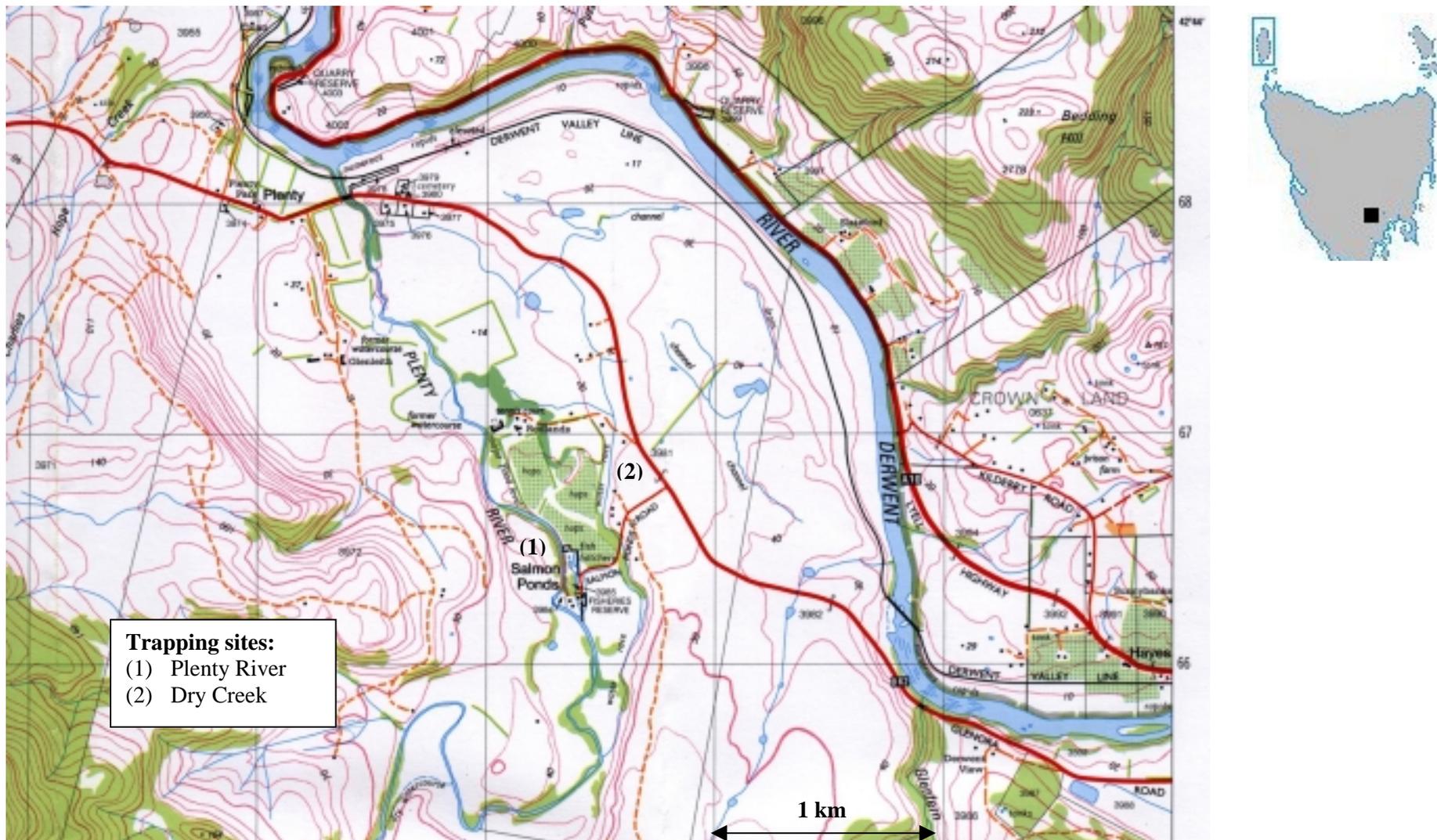


Fig. 2-1: Study Site Plenty River, Salmon Ponds, southeast Tasmania

Salmon Ponds is located in the Derwent River valley, which contains Tasmania's driest areas. On average, the area receives 550 mm of rain per annum. Rainfall is quite evenly spread throughout the year, although winter has more rain days. Summer daytime temperatures are mild. The average range is 20-23°C. Winter daytime temperatures average between 10-12°C. Water temperatures were found to range between 5-19°C. Frost is common in winter and spring with nighttime minimum temperatures falling to -5°C (Australian Bureau of Meteorology). Snowfalls are rare, and light when they occur.

2.1.2 Lake Lea, northwest Tasmania

Field studies were carried out at Lake Lea (41°30' S, 146°50' E, Photo 2-2, Fig. 2-3), a large dystrophic sub-alpine lake with karst features developed in Ordovician limestone located in the Vale of Belvoir in northwest Tasmania. The lake is shallow with an average depth of 2 to 3 metres at full winter levels and contains at least three deep holes at over 10 metres (Otley 1998). It has a number of associated permanent and ephemeral streams, pools and wetlands and is surrounded by different terrestrial vegetation communities including but-tongrass, 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 hectares with a catchment of 1480 hectares and an estimated volume of 2.6 million cubic metres (Cutler 1992).

The lake exhibits an unusual hydrological regime unique in Tasmania. Normally the lake flows northeastwards away from the Vale of Belvoir. However, during dry periods, it shrinks in volume and area, contracting on sinking points near its southwestern end. The humic waters support a range of aquatic and semiaquatic macrophyte and macro-invertebrate communities (Department of Lands, Parks and Wildlife 1989, Otley 1998). The water rat, the brown trout and the endemic burrowing crayfish *Parastacoides tasmanicus tasmanicus* as well as a number of water birds including black swans and black duck are also known to share the lake with the platypus (Department of Lands, Parks and Wildlife 1989, Otley et al. 2000 and personal observation). Although there

have been few scientific studies of the fauna in the area it seems reasonable to assume that the unique nature of the lake and associated habitats that make up its surrounding catchment would support a high diversity of endemic fauna.



Photo 2-2: Lake Lea, northwest Tasmania

The surrounding Vale of Belvoir area (Photo 2-3) is one of the most extensive montane grasslands in Tasmania and has a high priority for conservation, with natural, cultural, historical and aesthetic value (Gilfedder 1995). The vale area includes a variety of high altitude landforms and a complex mosaic of vegetation types. The flat valley floor and lower slopes contain large areas with limestone soil occupied by poa ssp. tussock grasslands. On the steep side slopes of the valley there is an abrupt transition, associated with changing soil type, to buttongrass (*Gymnoschoenus ssp.*) tussock sedgeland, eucalypt open forest (*Eucalyptus subcrenulata*) or *Nothofagus cunninghamii* closed forest (Register of the National Estate Database). The landscape of the Vale has been described as “almost monochromatic with tonal variations arising from shading on the hillocks and mounds” (Department of Lands, Parks and Wildlife 1989).

Generally, Lake Lea and the Vale of Belvoir experience mild summers and cold wet winters. The area receives a mean of 1600 mm rain per annum. On average, there are only 62 clear days per year. The highest monthly rainfall occurs in July and August. January and February are generally the driest months. The area is subject to severe weather. In winter, cold fronts crossing from the west bring heavy rainfalls and gale-force winds. Commonly this is associated with snow and hail, which is generally heaviest in late winter and early spring (Department of Lands, Parks and Wildlife 1989).



Photo 2-3: Vale of Belvoir, northwest Tasmania (Lake Lea in background)

Water and air temperatures at Lake Lea were recorded in two-hour intervals for the duration of this study using archival tags (HOBO Thermocouple logger and Stowaway Temperature Logger, Onset Computer Corp., USA, see App. C). Water temperature was measured directly in the lake close to site 3 (see Fig. 2-3) while air temperature was taken in a wind shaded forest patch nearby. Air temperatures ranged between -4°C and 31°C and water temperatures between 0°C and 29°C (Fig. 2-2). Relative lake level was measured in

1999. Averaged over summer and winter months, lake level was 45 and 58 cm higher in winter 1999 than in summer 1998/99 and 99/00, respectively. Also, cloud cover and weather conditions were recorded during the field trips directly at the lake. For all other times, weather data (cloud cover, rainfall [mm], air temperature) were obtained from Parks and Wildlife Service Tasmania collected by staff at the Visitor Centre, Cradle Mountain National Park.

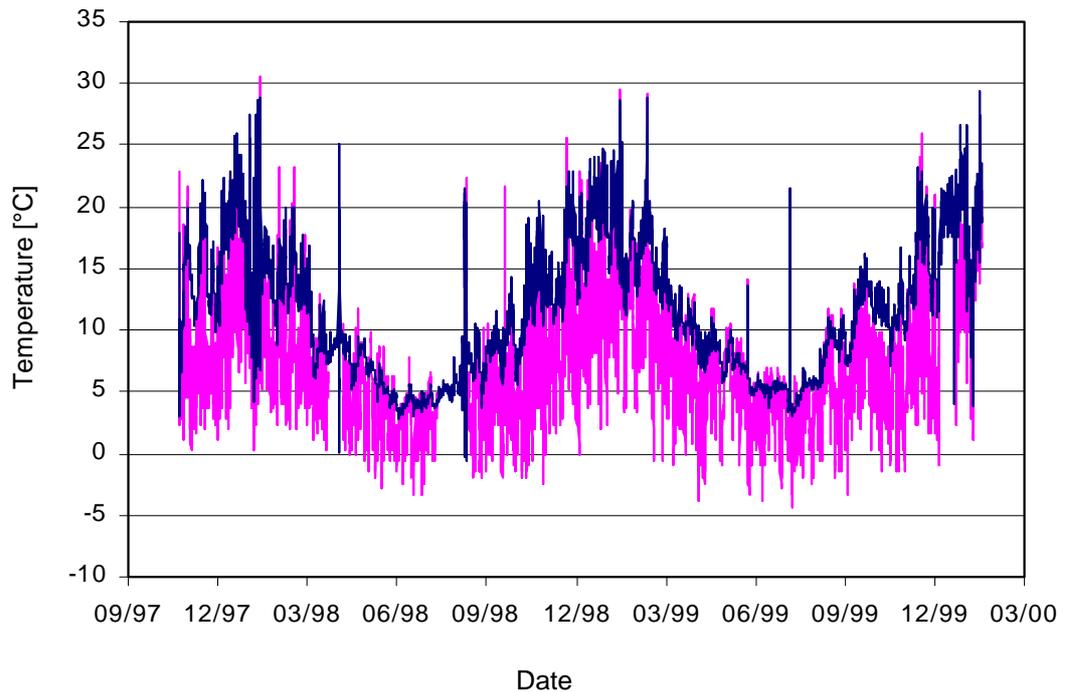


Fig. 2-2: Air (red) and water temperatures (blue) at Lake Lea from November 1997 to January 2000

Lake Lea and its tributaries were listed on the Register of the National Estate in 1982 because of their scientific and aesthetic qualities (Department of Lands, Parks and Wildlife 1989). Kirkpatrick and Tyler (1988), in their review of wetlands of significance in Tasmania, listed Lake Lea as having a high conservation priority. Despite this national recognition of its natural values the lake and its catchment has been disturbed by a number of developments since its listing, in particular road building and consequently increased recreational trout fishing activity as well as increasing tourist numbers.

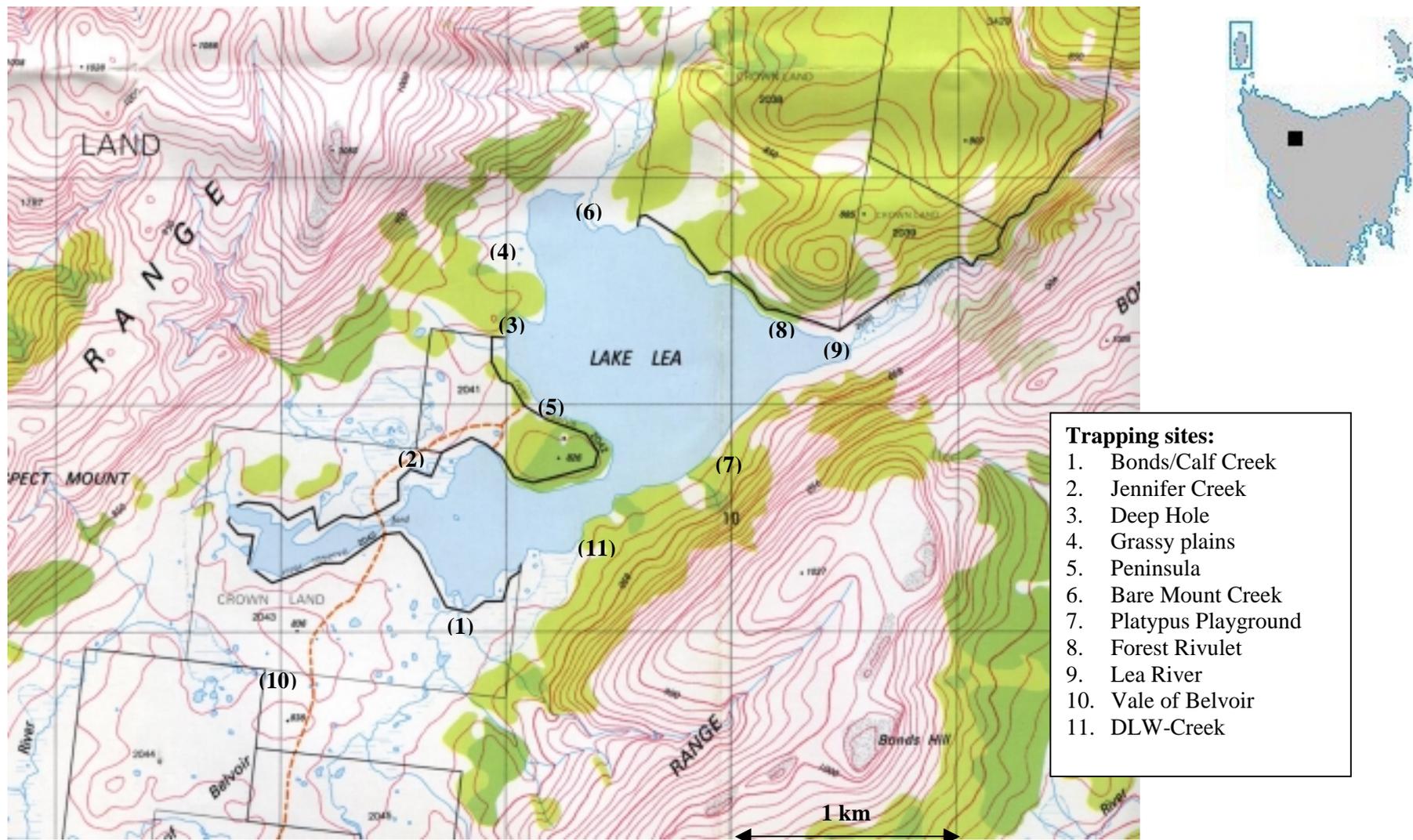


Fig. 2-3: Study Site Lake Lea, northwest Tasmania

2.2 Field methods and animals

2.2.1 General capture and handling methods

Platypuses for this study were captured following the methods outlined in Grant and Carrick (1974) and Serena (1994) (Permits to take protected wildlife Nos. FA 96196, 98004 & FA 99112, Department of Parks, Wildlife and Heritage, Hobart, Tasmania; Exemption Permits Nos. 97/14, 98/12 & 99/59, Inland Fisheries Commission, Hobart, Tasmania). Unweighted and partially weighted gill nets (50 and 15 m in length and 2 m in depth) were set in larger creeks and water bodies (Photo 2-4) while standard fyke nets with their distal ends staked several centimetres above water level were used in small creeks (Photo 2-5). In most cases, the nets were set in the afternoon and retrieved around midnight. Some early morning netting sessions were performed. All nets were checked at least every 20 minutes.

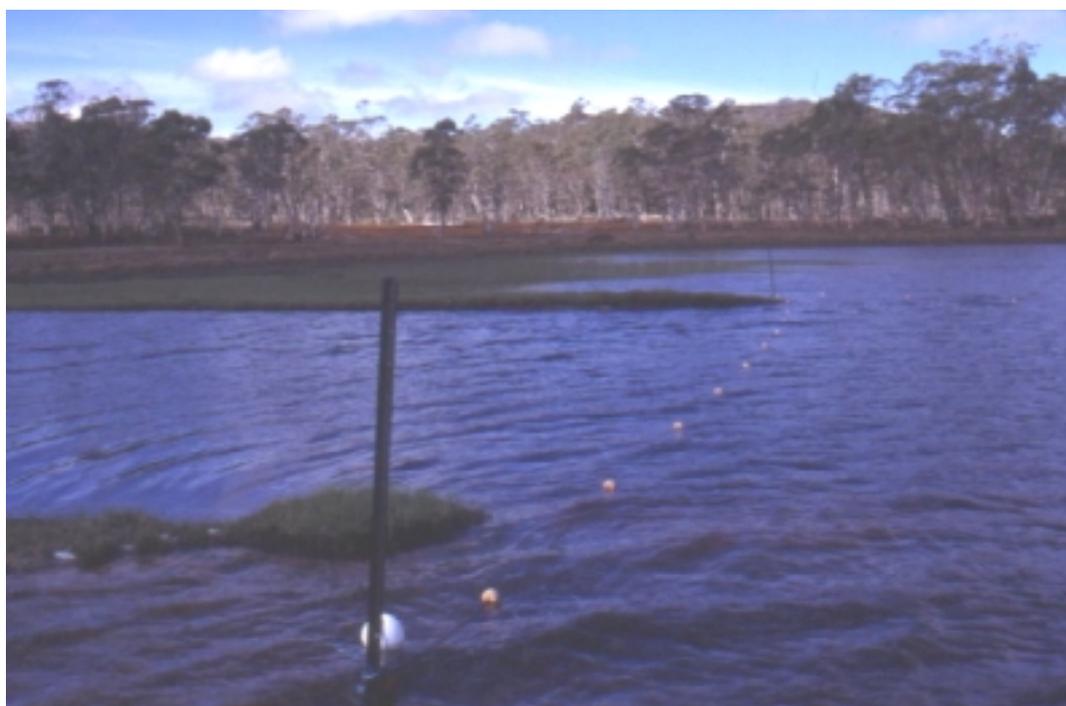


Photo 2-4: Gill net set at Lake Lea

Captured animals were marked with passive transponder tags (Trovan, Central Animal Records, Victoria) placed subcutaneously between the scapulae (Grant and Whittington 1991). Individuals were weighed using a spring balance (Salter, Australia). Body length was assessed with a measuring tape while holding the animal at the tail. Bill width and length (with and without shield) of the animals were measured. Sexual status and age class were identified based on spur and spur sheath morphology as well as body mass (Temple-Smith 1973, Serena 1994).



Photo 2-5: Fyke net set close to Lake Lea

Body condition was assessed by means of a standard tail-fat index (Grant and Carrick 1978, details see Appendix A). The reproductive status (lactating or non-lactating) of females was determined in some animals by an intramuscular injection of 0.3 ml synthetic oxytocin (5 I.U., Syntocin, Sandoz), which induces milk letdown (Grant et al. 1983).

2.2.2 Salmon Ponds animal details

From July 1997 to September 1998 a total of 27 platypuses (21 individuals) were captured during 20 trapping sessions in the Plenty River at Salmon Ponds and in Dry Creek, a water course running close to Salmon Ponds into the Plenty River (Fig. 2-1). Twelve of these individuals were brought into captivity for the measurement of oxygen consumption during various types of activity (see Chapters 3, 4 & 5).

Trapping sessions at Salmon Ponds lasted for an average of 5.7 hours. Total trapping time during the study period was 102.5 hours. Catch per net hour averaged 0.23 (range: 0.0 - 0.40) for gill nets (one net hour = 1 x 50 m net in water for one hour, Grant et al. 1992) and at 0.07 (range: 0.0 - 0.25) for fyke nets (one net hour = 1 fyke net in water for one hour). Capture times ranged from 6 p.m. through to 4 a.m.

The overall mean body mass for adult males and adult females captured at Salmon Ponds was 1.86 kg (SD=0.14, n=12, range: 1.62 - 2.00 kg) and 1.24 kg (SD=0.08, n=7, range: 1.09 - 1.35 kg), respectively. Body mass was significantly different between the sexes (t-test, $t=13.242$, $p<0.001$). Insufficient numbers of animals were obtained to assess any monthly or seasonal differences in body mass. Two subadults, one female (mass 1.26 kg, age approx. 9-12 months) and one male (mass 1.71 kg, age app. 9-12 months) were caught, both born in 1997. No lactating females were captured. Recapture rate was 22 %. Animal details are summarised in Tab. 2-1. Details of platypuses brought into captivity are shown in Tab. 3-1.

<i>Sex</i>	<i>Mass</i> [kg]	<i>Body length</i> [cm]	<i>Bill width</i> [mm]	<i>Bill length</i> [mm]	<i>Bill length</i> (+shield) [mm]	<i>n</i> SP/DC
male	1.85 (0.13)	52.8 (2.6)	49.0 (1.0)	55.9 (1.3)	74.7 (2.0)	9/3
female	1.24 (0.08)	46.8 (1.7)	44.1 (2.7)	49.0 (2.5)	68.2 (3.0)	5/2

Tab. 2-1: Details of adult platypuses caught at Salmon Ponds (SP) and Dry Creek (DC); means and standard deviations (in brackets) shown

Qualitative information on diet was obtained by collecting cheek pouch samples from 11 individuals and then identifying the diet fragments in the laboratory following the methods of Faragher et al. (1979) in collaboration with Dr. Jean Jackson and Karen Richards, School of Zoology, University of Tasmania. Cheek pouch sample fragments were identified with the aid of a reference collection of potential food items collected using standard macroinvertebrate sampling techniques. Analysis shows that platypuses in the area feed on a range of benthic macroinvertebrates with caddis fly larvae (*Trichoptera*) forming a major part of their diet (45% occurrence, Fig. 2-4; 64% dominance, Fig. 2-5) as they do in most places (e.g. Faragher et al. 1979, Grant 1983, Grant 1983a, Munks et al. 2000). Other relevant food items were Dipteran larvae (notably those of chironomids), Ephemeroptera, Gastropoda and crustaceans (amphipods and *Parastacidae*).

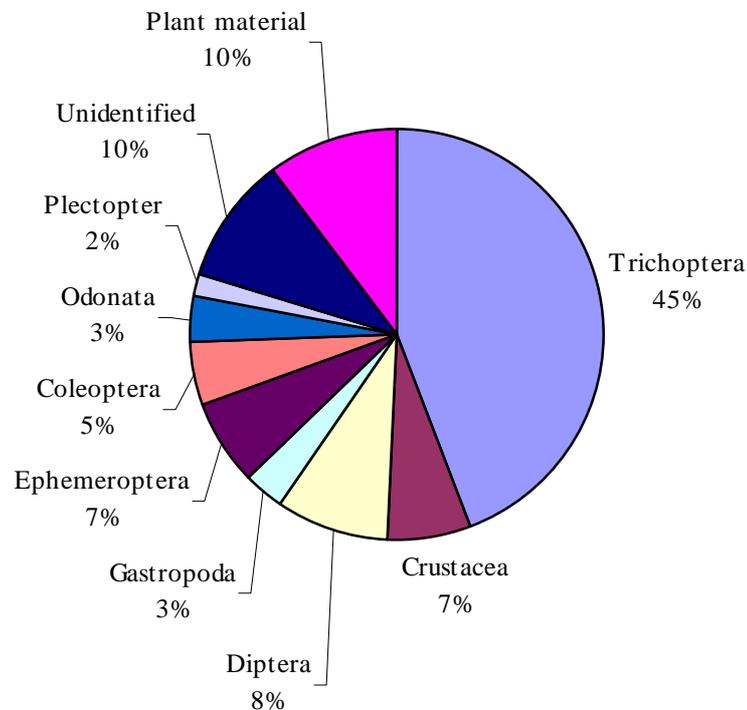


Fig. 2-4: Proportions of food items (% occurrence) identified in cheek pouch samples of platypuses caught at Salmon Ponds (n=11)

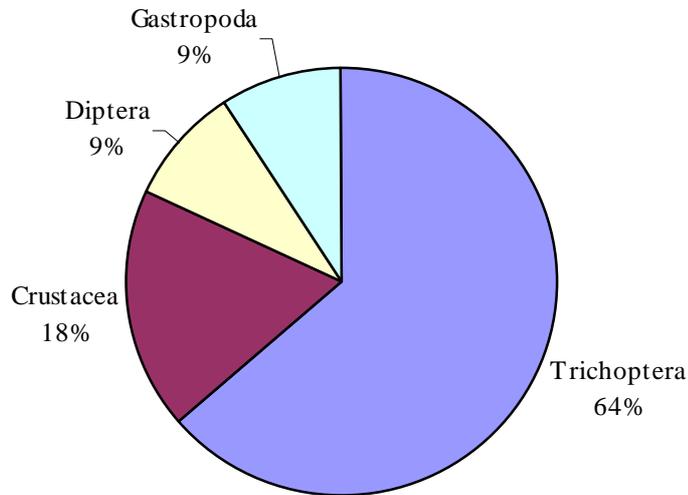


Fig. 2-5: Proportions of food items (% dominance) identified in cheek pouch samples of platypuses caught at Salmon Ponds (n=11)

2.2.3 Lake Lea animal details

From January 1998 to January 2000 a total of 197 platypuses (52 individuals) were trapped at Lake Lea as part of this study and concurrent studies (Munks et al. 2000, Munks et al., in prep. and unpublished data). Fifty-one of the captured animals (34 individuals) were equipped with combined data-logger-transmitter packages in order to investigate platypus foraging ecology (see Chapter 6). Eighteen field trips (about eight days long) were made covering all seasons. The animals were caught at 11 trapping sites around the lake (Fig. 2-3). The trapping sites were located at or close to the animals' burrow areas so that animals were mainly caught as they left or returned to their burrows. Trapping sessions lasted for an average of 6.6 h (maximum: 23.3 h). Total trapping time at Lake Lea during the study period was 870 hours.

Catch per net hour averaged 0.13 (range: 0.0 - 0.80) for gill nets (one net hour = 1 x 50 m net in water for one hour, see Grant et al. 1992) and 0.03 (range: 0.0 - 0.29) for fyke nets (one net hour = 1 fyke net in water for one hour) and was not significantly different between seasons (ANOVA, $p=0.062$). Capture times were variable with 75 % of all catches occurring between 6 p.m. and midnight. Catch per net hour was highest between 6 p.m. and midnight (Fig. 2-6). Seventy-seven percent of all individuals were caught at least twice with one platypus being captured 13 times (Fig. 2-7). Most animals, which had been caught previously, showed net avoidance behaviour.

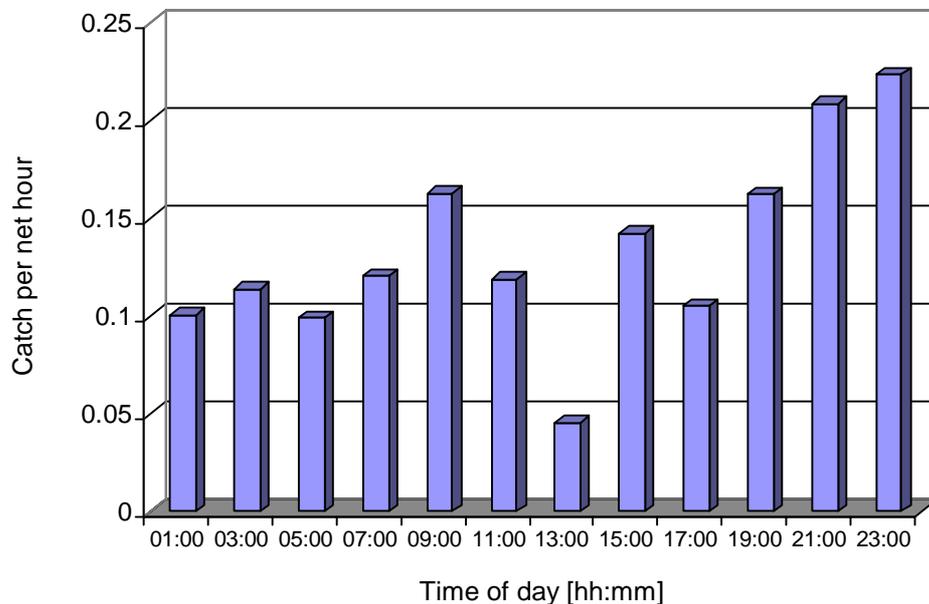


Fig. 2-6: Platypus captures per net hour at different times of the day at Lake Lea (n=197)

The overall mean body mass for adult males and adult females caught at Lake Lea between January 1998 and January 2000 was 2.10 kg (SD=0.31, $n=30$, range: 1.50 - 2.69 kg) and 1.47 kg (SD=0.11, $n=15$, range: 1.15 - 1.63 kg) for male and female animals, respectively. Body mass was significantly different between the sexes (t-test, $t=57.492$, $p<0.001$). However, body mass of adult male and female platypuses was not found to vary significantly between seasons (ANOVAs, $p=0.121$ and $p=0.208$, for male and female platypuses, re-

spectively). There was no significant seasonal difference in the condition of the adult animals as indicated by the tail fat index (ANOVA, $p=0.174$ and $p=0.168$, respectively). Animal details are summarised in Tab. 2-2.

<i>Sex</i>	<i>Mass</i> [kg]	<i>Body length</i> [cm]	<i>Bill width</i> [mm]	<i>Bill length</i> [mm]	<i>Bill length</i> (+shield) [mm]	<i>n</i>
male	2.10 (0.31)	56.3 (3.3)	50.2 (2.3)	57.3 (3.3)	77.9 (3.9)	30
female	1.47 (0.11)	50.1 (2.1)	44.4 (1.5)	52.5 (2.1)	70.3 (3.3)	15

Tab. 2-2: Details of adult platypuses caught at Lake Lea; means and standard deviations (in brackets) shown

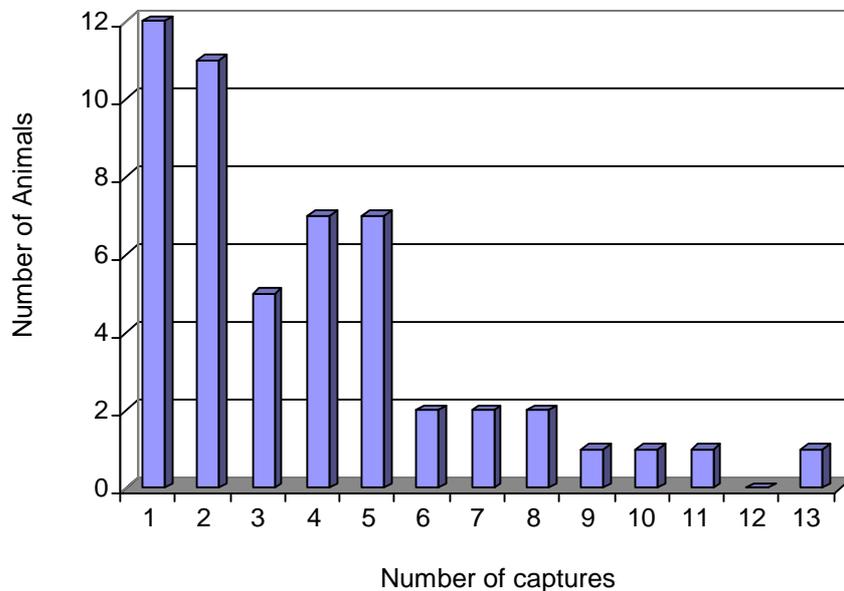


Fig. 2-7: Number of recaptures of individual platypuses at Lake Lea from January 1998 to January 2000 (n=52)

One lactating female, five juveniles and two subadults were caught in 1998. In 1999 two juveniles were caught and none in January and February 2000. Spur and spur sheath morphology indicated that three male and three female platypuses were born in 1997, one male in 1998 and two males in 1999. Body mass of juveniles ranged from 1.28 to 1.71 kg and from 1.24 to 1.31 kg for males ($n=4$) and females ($n=3$), respectively. The mating season at Lake

Lea appears to be later than in mainland populations. Estimated from the approximate age of male juveniles, Munks et al. (2000) suggested that mating season lasts from October to February with young emerging around April/June. However, the age of the juveniles caught during this study suggest that mating season at Lake Lea already starts in August (approx. one month later than in mainland habitats, Grant 1995) and lasts until the end of November. Correspondingly, lactation season is suggested to last from November to April (see Chapter 6.4.14, Fig. 6-21).

In a number of studies in the past, social units have been identified in platypus populations consisting of a group of resident and a number of transient individuals (e.g. Grant et al. 1992, Grant 1992a). Accordingly, at Lake Lea a resident population (i.e. at least one year between first and last catch) of 28 animals was observed (13 females, 15 males) while 24 transient individuals (5 females, 19 males) stayed temporarily at the Lake (i.e. less than one year between first and last catch). The percentage of transient animals captured was highest during the mating season in spring with 58 % of transient and 42 % of resident animals captured (Fig. 2-8).

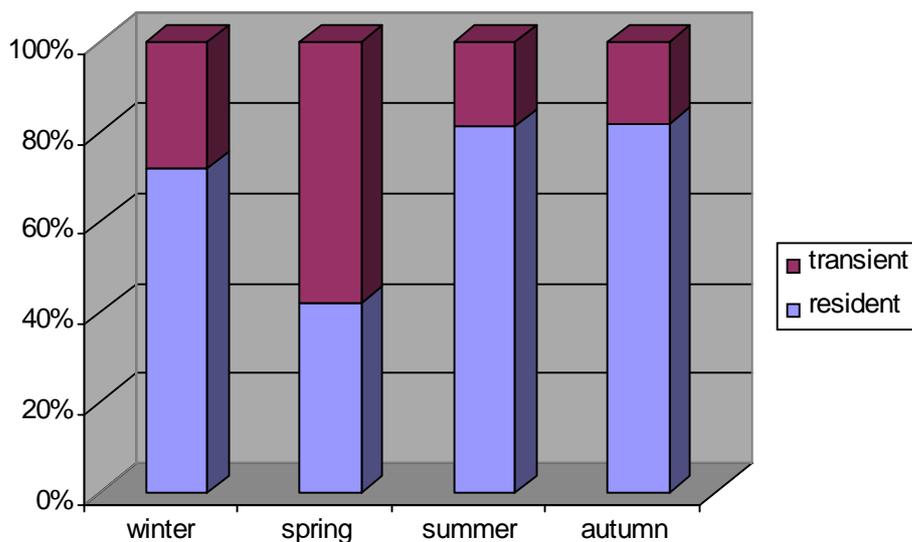


Fig. 2-8: Seasonal incidence of captures of resident and transient animals at Lake Lea (n=197)

Within the group of the resident platypuses, 15 platypuses (54 %) were caught at more than one trapping site suggesting the use of multiple burrows. Some animals were caught at up to three sites during this study with females being more variable in their site preference (Fig. 2-9).



Fig. 2-9: Percentage of resident platypuses using a single and multiple burrow sites at Lake Lea (n=28, determined from trapping locations)

Analysis of the cheek pouch samples from 20 females and 13 males at Lake Lea show that platypuses in the lake feed on a range of benthic macroinvertebrates with caddis fly larvae (*Trichoptera*) forming a major part of their diet (Munks et al. 2000, Munks et al. in prep.). In addition, the endemic burrowing crayfish *Parastacoides tasmanicus tasmanicus* found on the lake floor is an important food item. Preliminary results suggest that there are differences in diet selection between males and females and seasons (Munks et al. 2000, Munks et al. in prep.).

2.2.4 Comparison between habitats

The two sites visited during this study show very different habitat characteristics. Accordingly, considerable differences in size and mass of platypuses between the two habitats were observed. Both male and female platypuses captured at Lake Lea were significantly heavier than those trapped at Salmon Ponds (t-tests, $t=3.263$, $p=0.001$ and $t=4.884$, $p<0.001$, for male and female platypuses, respectively). The different climatic conditions and elevations (Lake Lea: 820 m, Salmon Ponds: 20 m) are a possible reasons for this observation. However, platypus body mass varies considerably between different sites in Tasmania independent of altitude (Tab. 2-3). Therefore, habitat productivity is likely to be the main factor, which determines platypus body mass (also Munks et al. 2000, Grant and Temple-Smith 1983). Yet, no data on the productivity of the Plenty River, Lake Lea or any other site mentioned in Tab. 2-3 were available.

<i>Site</i>	<i>male</i> [kg] (SD)	<i>female</i> [kg] (SD)	<i>n (m/f)</i>	<i>Catch per net</i> hour	<i>Altitude</i> [m]
Brumbys Creek, Cressy*	2.50 (0.28)	1.49 (0.17)	22/12	0.08	100-300
Mersey River, Weegema*	1.90 (0.14)	1.22 (0.16)	2/5	0.14	100-300
Emu River, Burnie*	2.12 (0.32)	1.20	3/1	0.23	<100
Salmon Ponds, Plenty	1.85 (0.13)	1.24 (0.08)	12/7	0.23	20
Lake Lea	2.10 (0.31)	1.47 (0.11)	30/15	0.13	820

Tab. 2-3: Comparison of platypus body weights recorded in Tasmania (*data from Connolly and Obendorf 1998)

In accordance with earlier studies (Burrell 1927, Griffiths 1978, Grant and Temple-Smith 1983) male platypuses at both study sites were found to be significantly heavier than female platypuses. Yet, no significant seasonal differences in the mean body mass of adult males and females were found at Lake Lea (see also Munks et al. 2000). This is in contrast to mainland studies in lotic

waters where either males or females lose weight in the winter months and body mass is highest in the summer (Grant and Temple-Smith 1983).

Catch per net hour was lower at Lake Lea than in the Plenty River at Salmon Ponds. Connolly and Obendorf (1998) suggested that low platypus capture rates are a consequence of more frequent and longer netting sessions. Indeed, Lake Lea was netted more frequently during this study and net avoidance behaviour was more often observed than at Salmon Ponds. Netting platypuses also appeared more difficult in the lake system because animals seemingly had more possibilities to avoid the nets due to the larger water body.

3 Maintenance of platypuses in captivity

3.1 Introduction

Ever since the first discovery of platypuses in Australia, there has been an interest in holding them in captivity for exhibits or for scientific reasons. However, early attempts to keep platypuses in captivity failed due to a lack of understanding of the animals' requirements (Grant et al. 1977). Bread, milk and rice were common in the diets offered to the animals which were even sometimes kept as house pets with no access to water (Burrell 1927, Grant et al. 1977).

As a consequence, in early attempts animals commonly died. Whittington (1991) described the survival rate of platypuses housed in zoological institutions as poor and stated that the probability of survival beyond one year in the 1980s remained less than 25 % for captive platypuses. Grant et al. (1977) and Carrick et al. (1982) reported the death of two platypuses during initial attempts to maintain the species in captivity. Later however, these and other authors managed to keep several animals in captivity for prolonged periods, also under experimental conditions.

Today, the animal is kept with some success in a number of sanctuaries across Australia. Platypuses have been exhibited in the Bronx Zoo, New York, USA, and the Budapest Zoo, Hungary (Grant et al. 1977) and have lived for up to 21 years in captivity (Whittington 1991).

Perhaps the ultimate measure of the quality of captive maintenance of a species, however, is breeding success (Faragher et al. 1979). In this respect, platypuses have only been successfully maintained twice, once by David Fleay in the 1940s (Faragher et al. 1979) and recently when two platypuses were born at Healesville Sanctuary, Victoria. Clearly, there is still urgent need for research into the captive needs of platypuses to successfully maintain them in holding facilities in the future.

3.2 Captive methods

3.2.1 Animal details, maintenance and food

Twelve of the 21 individual platypuses caught in the Plenty River at Salmon Ponds, Tasmania (see Chapter 2) were studied in captivity between July 1997 and September 1998 in order to determine their energy consumption during different activities (see Chapter 4 & 5). The animals (6 females, mean body mass 1.20 kg, SD=0.09; 6 males, mean body mass 1.84 kg, SD=0.17; for details see Tab. 3-1) were held at the University of Tasmania animal house for 7 to 11 days each in a specially designed platypussary based on the design of Manger and Pettigrew (1995). Only one individual was held at any one time. Platypuses were mainly fed live mealworms, red compost worms and tiger-worms. Some animals were offered crickets, defrosted yabbies (*Cherax quadricarinatus*) and brown trout fingerlings.

3.2.2 Swim tank details

The platypussary (Fig. 3-1) consisted of a fibreglass tank (1.4 metres high, 2 metres in diameter, water depth 90 cm) connected to a swim canal (3 metres long, water depth 50 cm) and an artificial burrow. Water temperatures ranged between 8°C in winter and 21°C in summer. The water was constantly renewed and circulated by a swimming pool pump (Onga 600 Series) through a sand filter (Onga Pantera) at a rate of 275 l min⁻¹ while the tank level was adjusted by an overflow. Transparent plastic sheeting just beneath the surface of the water in the tank and swim canal prevented the platypuses from surfacing over most of the tank and canal surface. The animals were only able to surface and breathe in three respiration chambers constructed from transparent plastic sheeting, one at each end of the canal (Volume: 18.7 l) and one at the entrance to the burrow (Volume: 100 l). A wooden platform placed in the chamber at the burrow entrance, just above water level, allowed the platypuses to sit out of the water and groom. The tank was partly uncovered during non-experimental conditions to allow the animals more freedom of movement.

Identity	Sex	Age (Spur class*)	Capture Date	Site	Capture mass [kg]	Release mass [kg]	Days in captivity	Tail fat*	Moult class*	Body length [cm]	Bill (width / length / length + shield) [mm]
00-01C6-17AF	f	adult	08/24/97	SP	1.10	1.04	7	3	very light	47	44.4 48.2 67.2
00-0124-ABB7	f	adult	03/31/98	SP	1.20	1.09	8	2	very light	50	41.2 47.5 64.0
00-0125-F478	f	adult	05/12/98	SP	1.09	1.03	7	3	very light	44	42.0 48.0 64.0
00-01CA-6B5A	f	adult	06/23/98	SP	1.25	1.25	7	2	light	47	50.4 43.7 67.9
00-012E-8017	f	adult	08/11/98	SP	1.32	1.27	8	3	moderate	46	45.3 51.1 72.6
00-01CA-6C32	f	adult	09/18/98	DC	1.26	1.19	7	3	very light	47	43.1 50.8 68.2
00-01F9-D8B1	m	adult (E)	07/14/97	SP	1.85	1.84	10	2	very light	53	48.7 53.3 74.2
00-01D2-9414	m	adult (E)	09/01/97	SP	1.91	1.90	11	2	very light	48	47.2 55.9 75.2
00-0145-3476	m	adult (E)	10/06/97	DC	2.08	1.77	7	3	very light	54	51.0 57.9 78.3
00-01D3-1FC7	m	adult (E)	11/29/97	SP	1.69	1.74	8	2	none	55	48.7 56.1 72.5
00-0125-263E	m	adult (E)	01/31/98	SP	1.62	1.59	9	2	very light	52	47.7 56.3 75.3
00-0145-3476	m	adult (E)	09/10/98	SP	1.91	1.89	7	2	very light	54	51.0 57.9 78.3

Tab. 3-1: Captive animal details (SP=Salmon Ponds, DC=Dry Creek, *explanation see Appendix A)

The artificial burrow consisted of a wooden tunnel (13 m long, 200 mm high x 300 mm wide) approximating the natural burrow length of wild platypuses (Burrell 1927, Manger and Pettigrew 1995). Two nesting boxes (300 mm high x 400 mm wide and long) were built in as part of the tunnel and dried sea grass was provided as nesting material. To enter the tank from the artificial burrow the animals had to pass through a rubber tube ($\text{\O} 15 \text{ cm}$). While inactive (generally over the day), the platypuses were locked in the artificial burrow. During occasional checks, they were mostly found to be sleeping in a curled up position.

3.3 Results

Platypuses placed in the platypussary learned within two nights where they could surface to breathe and how to get from the swim tank into the artificial burrow and vice versa. Foraging during the active period could be divided in three phases. After diving to the bottom with obvious effort and fast movement of the propelling forelegs (phase-1), the animals foraged along the tank bottom moving their bill from one side to the other in a characteristic sweeping movement while searching for food (phase-2, see for comparison Manger and Pettigrew 1995, Fish et al. 1997). Finally, they surfaced by simply stopping their movement and returning to the surface through the positive buoyancy of their bodies (phase-3). Under the water, the eyes were closed and the animals were always in motion, with fast foreleg movements counteracting the upward force on the body (see for comparison Burrell 1927, Scheich et al. 1986, Grant 1995). When disturbed, animals either swam to a different respiration chamber or performed a distinct behaviour called wedging (Grant 1995), i.e. resting under water underneath the plastic sheeting for up to 5 minutes.

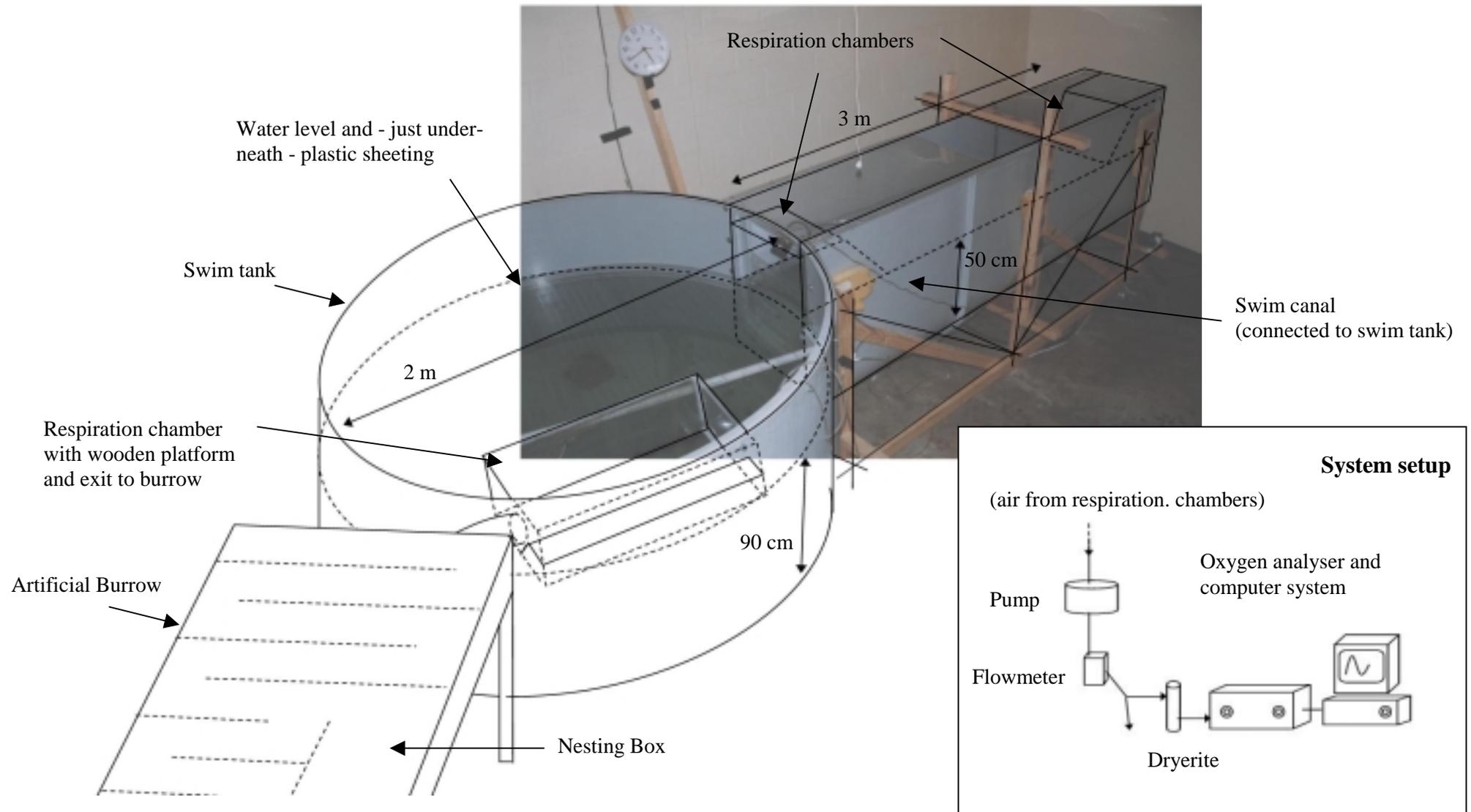


Fig. 3-1: Platypussary and system setup for measurement of oxygen consumption

Active dives were between five and 77 seconds duration and averaged 23.9 s (SD=3.97, n=12) with no significant differences in dive duration between male and female platypuses ($t=0.899$, $p>0.05$). Probably due to the free availability of food in the tank, only about ten dives per hour were performed. In between, the platypuses either processed their food or enjoyed extended resting periods at the water surface or on the platform. When on the platform, in most cases the animals started to groom themselves immediately, always using the hind legs only. Grooming in water was a rare event.

Platypuses ate on average 170.5 g of food per night (SD=16.9, n=12) with no significant differences in food consumption between males and females ($t=-0.3088$, $p>0.05$). Most animals did not feed in the first night after capture. An initial drop in body mass of about 5 % was observed in the first two days after capture. Body mass stabilised or increased after day 3 of captivity (Fig. 3-2). Whilst the platypuses collected compost and mealworms from the bottom of the tank with ease, more energetic hunting behaviour was observed in two occasions. The first involved a platypus accepting defrosted yabbies as food (and eating up to 31 per night), which it then transported to the water surface in its bill and subsequently separated shell and flesh of the crustacean by fast movements of its head. The second involved a platypus fed with live brown trout fingerlings, which provoked an enthusiastic hunting behaviour. The animal detected the little fish larvae underwater with ease and hunted them down with previously unseen speed and skill.

After seven to nine days of captivity most platypuses became increasingly inactive and sluggish and were released back in the wild. None of the animals died in captivity. Some of the twelve animals used for the experiments became quite tame in captivity but most of them stayed suspicious and cautious. A thirteenth animal (not included in analysis) had to be released soon after capture because it did not eat at all.

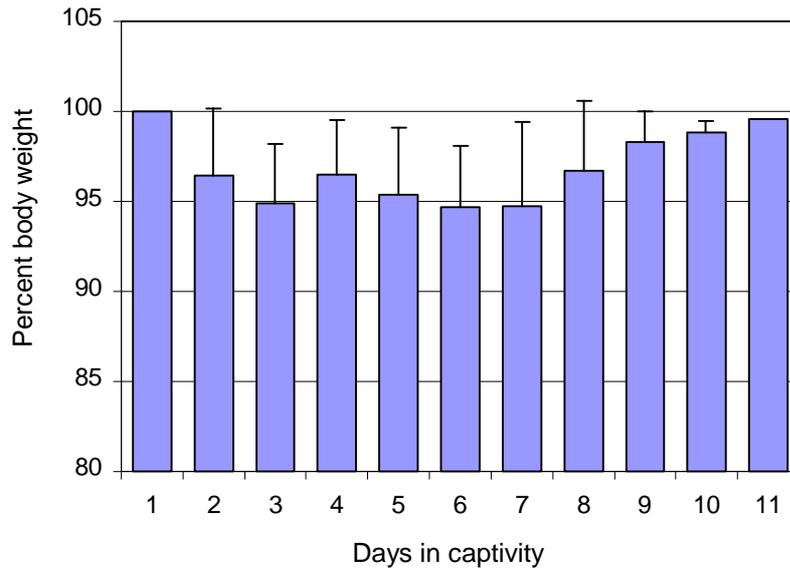


Fig. 3-2: Changes in body mass in captive platypuses (n=12, bars show standard deviation)

3.4 Discussion

Platypuses are known to eat a variety of food items in captivity and some reports suggest that the weight of food taken by a platypus per day can amount to over half its own body mass. Burrell (1927) for example reports that one of his captive animals consumed 70 earthworms, 10 ground grubs and 600 salt water prawns in only 72 hours. Daily diets given in other captive experiments included earthworms, mealworms, eggs, yabbies, frogs or woodlice (Collins 1973, Grant et al. 1977). The amount of food eaten by the animals during these studies ranged between 500 and 950 g per day (Grant et al. 1977, Carrick et al. 1982). Krueger et al. (1992) reported prey quantities in captivity representing between 14.9 and 27.8 % of the animals' body mass, which converts to between 224 and 417 g food per day for a 1500 g platypus.

In this study, although food was abundant, platypuses ate on average only 170 g of food per night (95 and 138 g fresh matter $\text{kg}^{-1} \text{day}^{-1}$ for male and female platypuses, respectively). We suggest that the low activity levels in the

swim tank (on average only about ten foraging dives per hour) are a likely reason for the low food intake of our captive platypuses.

However, food requirements derived in this study were still higher than food requirements of platypuses foraging in the wild calculated by Faragher et al. (1979). Field metabolic rates derived in this study (see Chapter 8.3.2) suggest a mean food intake in the wild of 132 g fresh matter $\text{kg}^{-1} \text{day}^{-1}$, which is still much less than the huge quantities reported for captive platypuses by Grant et al. (1977) and Carrick et al. (1982). This supports the view that food intake of captive platypuses might have been overestimated by earlier authors, possibly as a consequence of the difficult quantification of food wastage.

An initial weight loss of platypuses after capture has been previously reported (Grant et al. 1977, Carrick et al. 1982). In this study, with one exception, platypuses regained and stabilised their weight after some days in the swim tank, a finding also reported by Faragher et al. (1979). The platypuses also turned out to be quite robust with regard to disturbances and daily routines. Reports that platypuses do not tolerate disturbance of their physical environment or management regime (Carrick et al. 1982) or that animals can be "easily killed by too much excitement" (Burrell 1927) could not be confirmed.

The need for Faraday shielding to reduce exposure to electrical fields postulated by Manger and Pettigrew (1995) could not be confirmed, at least for short periods of captivity. No shielding was provided in the experimental set-up in this study. Nonetheless, platypuses did not show signs of confusion or disorientation while foraging under water. However, it has to be stated that platypuses were kept only for up to 11 days and long-term effects of captivity on their condition and behaviour could not be investigated.

Faragher et al. (1979) noted the extraordinary ability of platypuses to escape due to their strong body, their streamlined shape and their "high degree of inquisitiveness". In this study, much effort was necessary to make the swim tank "platypus-proof". On several occasions platypuses were able to force their way out of the tank through very small gaps, but in all cases remained secure within the animal house.

Although platypuses did not show signs of physical changes other than the initial weight loss, the animals were found to change their behaviour profoundly during short-term captivity. While they foraged quite happily in the tank during the first days of the experiments, they increasingly became inactive and sluggish after a couple of days. Burrell (1927), reporting on one of the earliest attempts to keep platypuses in captivity, noted that the platypus seldom remained in the water longer than 10 to 15 minutes. Grant (1983) also reported that captive platypuses will only enter the water for short periods, when given free access to the water and to easily accessible food resources. Platypuses on display at Healesville Sanctuary and Taronga Zoo foraged only for 20-25 % (Krueger et al. 1992) and 6.6 % (Hawkins and Fanning 1992) of their time, respectively.

This reduction in foraging time, however, might not only be a consequence of easy food access but also a sign of inappropriate holding facilities. The static environment provided in this and other captive studies might not pose enough challenges for the animals. Possibly, not enough emphasis has been put on size and the environment provided in platypus holding facilities in the past, especially under experimental conditions. Useful for short-term observations under controlled conditions, the swim tank used in this study for example, although quite big compared to other facilities, clearly was not the optimum design for long term maintenance.

We suggest that the design of future holding facilities should draw on the results of ecophysiological and behavioural work on the platypus. For example, in the wild, the platypus' environment is constantly changing due to changes in water level and flow rate in lakes and streams (e.g. Grant 1995). In addition, in the wild food is much harder to access. Captive holding facilities should aim to mimic these conditions and the variation in habitats. More emphasis on sufficient space in holding facilities as well as more research on the husbandry requirements of the species in general is needed to improve captive maintenance of platypuses in future studies and exhibits.

4 Energetics of foraging and resting in the platypus

4.1 Introduction

Platypuses can spend long periods continuously foraging in water at nearly 0°C. Through anatomical and behavioural specialisation the animal can extremely well minimise loss of metabolic heat under these conditions. Grant and Dawson (1978b) showed that body temperature does not fall significantly during immersion in water at 5°C, while metabolic rate raises to only 3.2 times the resting level. By contrast, the water rat *Hydromys chrysogaster* cannot maintain T_b at water temperatures below 25°C (Dawson and Fanning 1981). It is tempting to speculate that, just as the platypus is better adapted to life in cold water than other semiaquatic mammals in terms of its insulation, it will also have a very low swimming metabolism.

The efficiency of the swimming mechanism and the adaptations to the aquatic environment of the platypus have been disputed in the past (e.g. Howell 1937). Like other semiaquatic mammals, the platypus has a body form that deviates considerably from the optimal design to minimise drag (Fish 1992). In addition, semiaquatic animals in general have higher energy costs for swimming (Fish 1982, Williams 1983a, Baudinette and Gill 1985, Williams 1989). However, Fish et al. (1997) suggested that the specialised rowing mode of the platypus results in very efficient swimming.

The objective of this part of the study was to further elucidate the extent of physiological adaptation to swimming that has occurred in the platypus. In addition, data on active metabolic rates of platypuses during foraging were expected to contribute to the creation of a time-energy budget for the species. A swim tank in conjunction with respirometry was used to determine energy consumption of the platypus while foraging, diving and resting. Compared to swim flumes where animals have to maintain an unnatural position or a certain speed, in a swim tank animals are able to select their own swimming speed and dive duration while all activities and gaseous exchange can be closely monitored (Culik and Wilson 1991, Culik and Wilson 1994, Bethge et al. 1997).

4.2 Materials and methods

4.2.1 Experimental setup

The energetic demands of the platypus were determined using flow-through respirometry in an open circuit system. Oxygen consumption while foraging, diving and resting in water was determined using the swim tank described in Chapter 3.2 and Fig. 3-1. Oxygen consumption while resting on land was determined using an additional respiration chamber. Twelve individual platypuses were studied in the laboratory (for details see Chapter 3.2). Experiments started on day three after capture.

For the experiments, only one of the three respiration chambers of the swim tank was connected to the respiration system (Fig. 3-1). The chamber was equipped with a mixing fan and was open to outside air. Air was drawn through the chamber by a pump at a mean flow rate of 20 l min^{-1} , measured by a mass flow meter (TYLAN model FM-380). A subsample of the air was dried and passed onto an oxygen analyser (Applied Electrochemistry Inc., Sunnyvale, California, model S-3A). Data from the oxygen analyser and the mass flow meter were sampled every 0.5 s using a Mac Lab (Analog Digital Instruments Pty Ltd, Castle Hill, NSW) and an Apple Macintosh Classic II Computer. The whole system was calibrated following Fedak et al. (1981) using known volumes of nitrogen. Mean measurement error was $<1\%$. The system was checked for leaks before each experiment.

Measurements were taken for an average of six hours. During the experiments, the platypuses were continuously observed by a video camera mounted over the swim tank connected to a VCR. Activity and dive duration of the animals were later derived from the videotapes. Only foraging bouts where all three phases of diving behaviour (see Chapter 3.3) were completed were used for analysis. Burrow access was closed after the animals had entered the swim tank at dawn and reopened after the experiments.

To determine the effect of externally-attached devices on the energy requirements of the platypuses, 6 animals were equipped with data-loggers (weight 40 g) in about one third of the experiments.

Resting rates in water were measured during naturally occurring resting periods of the animals in the swim tank. Only data from resting periods longer than five minutes were used for analysis. Oxygen consumption while resting on land was measured using an additional respiration chamber (Volume 28.3 l), constructed from transparent plastic sheeting, which was connected to the respiration system described above. The chamber had to be covered with hessian bags during the experiments since the animals did not settle otherwise. Data were taken only from fasted animals resting quietly for at least five minutes.

4.2.2 Data Analysis

To calculate the O₂-consumption a modification of the formula given by Woakes and Butler (1983) was used, which incorporates chamber volume and allows accurate measurement of fast changes in O₂-concentrations irrespective of the systems lag time:

$$VO_2 = (c_1 - c_2) \times V + [(c_1 + c_2 - 2 \times cb) / 2] \times (t_2 - t_1) \times Q$$

where VO₂ = O₂-consumption between t₁ and t₂ [l] (STPD), c₁, c₂ = fractional concentration O₂ at time t₁, t₂ [sec] leaving the chamber, cb = fractional concentration O₂ entering the chamber (0.2095), Q = flow-rate through the chamber [l s⁻¹], V = chamber volume [l].

Following Withers (1977), correction for the respiratory quotient (RQ) of the platypus was made (RQ=0.8, Brody 1945, Grant and Dawson 1978a, Fish et al. 1997). Correction for RQ yields:

$$VO_2 = (c_1 - c_2) \times V + [(c_1 + c_2 - 2 \times cb) \times (t_2 - t_1) \times V_E] / [2 \times (1 - (1 - RQ) \times cb)]$$

where VO₂ = O₂-consumption between t₁ and t₂ [l] (STPD), V_E = flow-rate measured behind the respiration chamber [l s⁻¹] (STPD), RQ = respiratory quotient (0.8).

To calculate the rate of oxygen consumption while diving in the swim tank O₂-consumption in the chamber was assumed to be identical to the platypus's resting values at the water surface. Accordingly, the resting metabolism in the chamber was subtracted from the total amount of oxygen consumed during the recovery period after each dive following Culik and Wilson (1991) and Bethge et al. (1997):

$$VO_{2(\text{FORAGE})} = VO_{2(\text{TOTAL})} - VO_{2(\text{REST})} \times t_{\text{SURFACE}}$$

where $VO_{2(\text{TOTAL})}$ = O₂-consumption between time of surfacing (t_1) and time of leaving the chamber (t_2) [l], $VO_{2(\text{REST})}$ = O₂-consumption rate for resting at the water surface [$l\ s^{-1}$] and t_{SURFACE} = time at the surface [s]. Conversion into $W\ kg^{-1}$ was made assuming a conversion factor of 20.11 kJ l⁻¹ of oxygen (Grant and Dawson 1978a) following

$$P = [VO_{2(\text{FORAGE})} \times \text{c.f.}] / [t \times m]$$

where P = foraging rate $P_{(\text{FORAGE})}$ [$W\ kg^{-1}$], c.f.= conversion factor [$kJ\ l\ O_2^{-1}$], t = dive duration [s] and m = body mass [kg].

Individual platypuses were tested multiple times in the experiments. To account for repeated measures, mixed multiple regressions were calculated where random effects represent differences between individuals. Statistical tests were also made using single factor or multiway factorial analysis of variance (ANOVA) with individual (n=12) as a random factor and the effects in question as covariates. For multiple comparison, the Tukey test was used. To test for differences between two means, standard t-tests were performed. Simple and multiple 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. Detailed statistical results for this chapter are shown in Appendix B-1.

4.3 Results

4.3.1 Resting metabolic rate in water and on land

The mean resting metabolic rate obtained from 10 platypuses in air was 2.54 W kg^{-1} ($\text{SD}=0.38$, $n=10$, equals $0.46 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$) and ranged from 2.08 W kg^{-1} (at 26°C ambient temperature) to 3.26 W kg^{-1} (at 10°C). Resting metabolic rates were significantly dependent on air temperature ($p<0.001$) but not on the weight of the platypuses ($p=0.052$, see App. B-1). Lower air temperatures caused higher resting rates. Similarly, heat production in water increased gradually as water temperature decreased.

The mean metabolic rate obtained from 10 platypuses resting on the water surface was 4.81 W kg^{-1} ($\text{SD}=0.91$, $n=10$, equals $0.86 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$) and ranged from 3.91 W kg^{-1} (at 21°C water temperature) to 6.39 W kg^{-1} (at 9°C). Resting metabolic rates in water were significantly dependant on water temperature ($p<0.001$), but not on animal-mass ($p=0.725$, see App. B-1).

Platypus resting metabolic rates in air respectively water are best predicted by

$$P_{(\text{REST})[\text{in air}]} = 0.035 T_{\text{a/w}} + 24.49 T_{\text{a/w}}^{-1} + 0.3 \quad (n=14, r=0.86) \quad (1)$$

and

$$P_{(\text{REST})[\text{in water}]} = 0.107 T_{\text{w}} + 61.77 T_{\text{a/w}}^{-1} - 1.48 \quad (n=47, r=0.81) \quad (2)$$

where $T_{\text{a/w}}$ = air/water temperature [$^\circ\text{C}$] and $P_{(\text{REST})}$ is in W kg^{-1} .

In the wild, platypuses wedge themselves occasionally under rocks and logs under the water surface, supposedly to hide in case of danger or emergency (Grant 1995). Occasionally, animals performed such 'wedging' behaviour in the swim tank underneath the plastic sheeting. On some occasions 'wedging' occurred close to one respiration chamber so that the platypus was able to stick its bill up above the water line to occasionally take a breath, a behaviour also observed in the wild under ice (Otley and Munks, personal com-

munication). Measurements for 'wedging' were obtained from those events in four animals. The mean metabolic rate for 'wedging' under water was 3.46 W kg^{-1} ($SD=0.46$, $n=4$, equals $0.62 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$) and varied with water temperature. Results are summarised in Fig. 4-1.

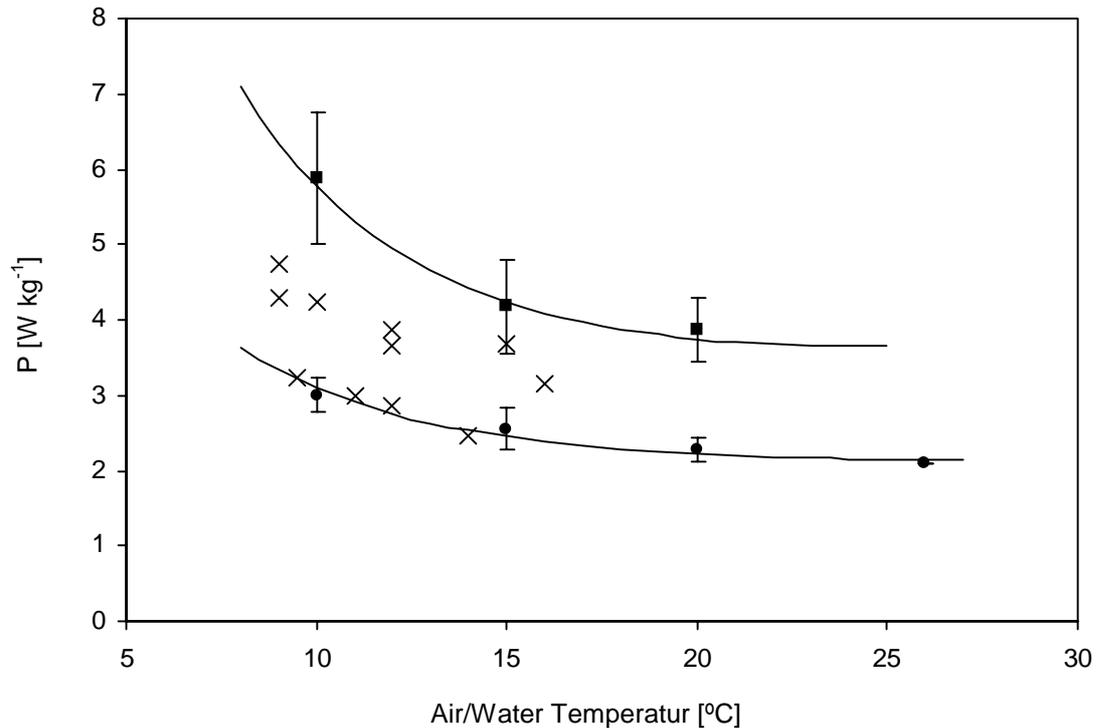


Fig. 4-1: Platypus resting metabolic rates in air and water, plotted as a function of air and water temperature respectively. Means \pm standard deviations shown. Circles = air, squares = water, crosses = wedging. Lines show predicted values.

4.3.2 Metabolic rate for foraging and subsurface swimming

To determine metabolic rate for foraging and subsurface swimming, 555 dives from 12 different platypuses were analysed. To account for repeated measures, a mixed multiple regression was calculated (grouping variable: individual, fixed effect: body mass, random effects: dive duration and water temperature, see App. B-1). Within as well as between individuals, foraging metabolic rate was significantly dependant on dive duration (within subjects:

$p=0.030$, between subjects: $p<0.001$) as well as on water temperature (within subjects: $p=0.032$, between subjects: $p=0.048$). Shorter dives required relatively more energy than longer dives, especially dives of less than 20 s duration. Also, foraging metabolic rate was significantly dependant on body mass ($p=0.018$). As trends within and between subjects were consistent, data were pooled for analysis.

Total energetic costs for foraging $C_{(\text{FORAGE})}$ [J kg^{-1}] and foraging metabolic rates $P_{(\text{FORAGE})}$ [W kg^{-1}] of platypuses are best predicted by

$$C_{(\text{FORAGE})} = (9.04 - 0.21 T_w - 0.90 m) t + 109.21 \text{ and}$$

$$P_{(\text{FORAGE})} = 9.04 - 0.21 T_w - 0.90 m + 109.21 t^{-1} \quad (n=555, r^2=0.61) \quad (3)$$

respectively, where T_w = current water temperature [$^{\circ}\text{C}$], m = body mass [kg] and t = dive duration [s]. Fig. 4-2 shows the total energy costs while foraging ($C_{(\text{FORAGE})}$) plotted as a function of dive duration. Fig. 4-3 shows foraging rates ($P_{(\text{FORAGE})}$) plotted as a function of dive duration. Shorter dives required relatively more energy than longer dives. Foraging rates of platypuses also increased with decreasing water temperature and with decreasing body mass of the animals.

To compare the metabolic rates of animals equipped with data loggers and those of animals without data loggers, data were standardised for water temperature, dive duration and body mass. The data loggers did not cause a significant increase in the mean foraging metabolic rate (t-test, $t=0.55$, $p=0.297$). To compare males and females we standardised the data for water temperature and dive duration only. Foraging rates for female animals (8.73 W kg^{-1} , $\text{SD}=0.22$, $n=6$) were significantly higher than for males (8.14 W kg^{-1} , $\text{SD}=0.40$, $n=6$, t-test, $t=-1.84$, $p=0.047$). However, if we test for differences between male and female animals independent of body mass, we do not find a significant difference in power requirements between the sexes (t-test, $t=0.24$, $p=0.407$). Therefore, different power requirements for male and female platypuses relate to differences in body mass rather than physiological differences

between the sexes. The mean foraging metabolic rate obtained from 12 platypuses was 8.48 W kg^{-1} (SD=0.66, n=12, equals $1.52 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$).

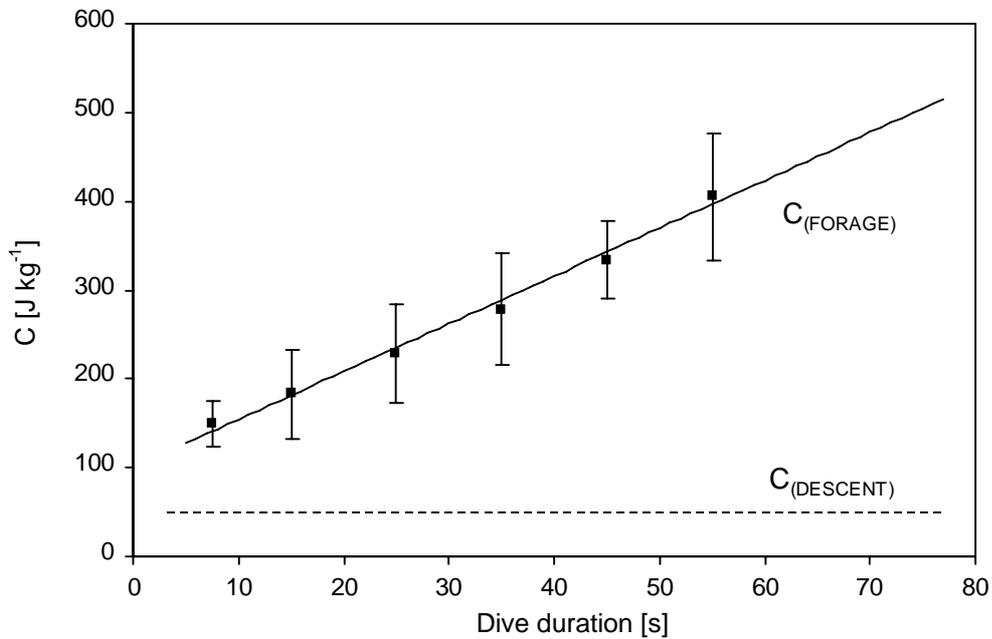


Fig. 4-2: Energetic costs of platypuses foraging in a swim tank, plotted as a function of dive duration (n=555). Means \pm standard deviations shown. Solid line shows prediction for $C_{(\text{FORAGE})}$; dotted line shows $C_{(\text{DESCENT})}$ (see text below)

To be able to compare power requirements for under water swimming in the platypus with other subsurface swimmers, the metabolic rate for subsurface swimming $P_{(\text{DIVE})}$ was estimated. In this study, the best estimation of $P_{(\text{DIVE})}$ is the energy requirements of platypuses foraging on the tank bottom (phase-2-behaviour, see Chapter 3.3). Assuming that the cost of resurfacing after the dive is negligible due to the positive buoyancy of the animals, $P_{(\text{DIVE})}$ can be obtained following $P_{(\text{DIVE})} = P_{(\text{FORAGE})} - C_{(\text{DESCENT})} / t$ where t is dive duration [s] and $C_{(\text{DESCENT})}$ [J kg⁻¹] is the total cost for diving vertically down to the bottom of the tank (phase-1). The latter behaviour was characterised by powerful strokes with the forefeet and high swimming speeds. Therefore, $C_{(\text{DESCENT})}$ can be best estimated following $C_{(\text{DESCENT})} = P_{(\text{MAX})} d v_{(\text{MAX})}^{-1}$ where $P_{(\text{MAX})}$ is the

maximum foraging rate observed in the tank (20.17 W kg^{-1}), $v_{(\text{MAX})}$ is the highest speed observed (0.43 m s^{-1}) and d is the water depth in metres. The mean metabolic rate $P_{(\text{DIVE})}$ for subsurface swimming was 6.71 W kg^{-1} ($\text{SD}=0.68$, $n=12$, equals $7.34 \text{ W kg}^{-0.75}$ or $1.20 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$).

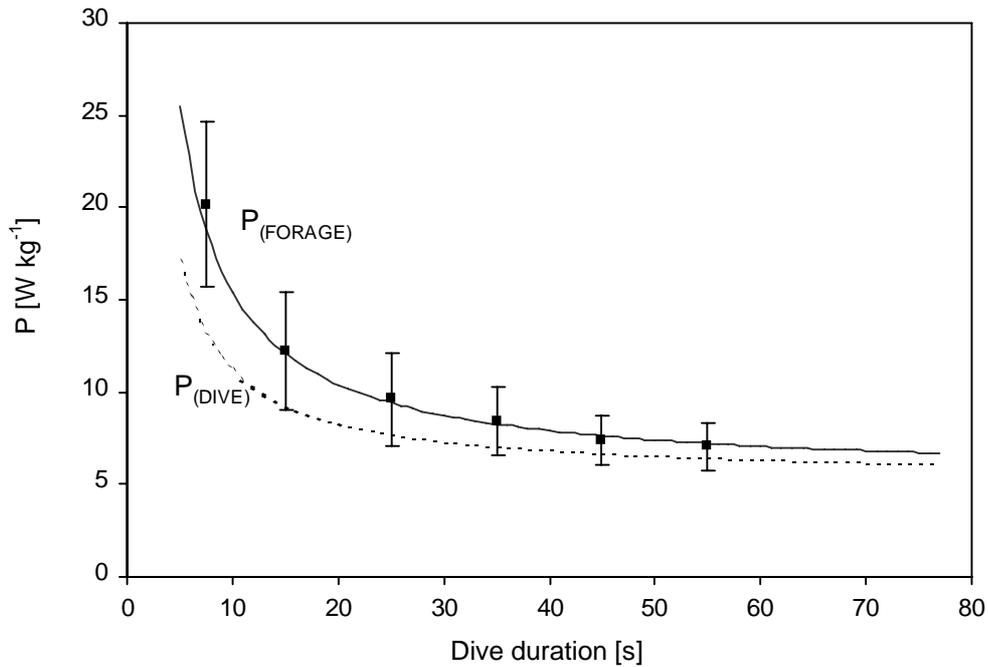


Fig. 4-3: Metabolic rates of platypuses foraging in a swim tank, plotted as a function of dive duration ($n=555$). Means \pm standard deviations shown. Solid line shows prediction for $P_{(\text{FORAGE})}$, dotted line for $P_{(\text{DIVE})}$ (see text)

4.4 Discussion

4.4.1 Instrument and experimental effects

In the wild platypuses live in a complex environment where size and depth of water bodies can change dramatically within days, where flow and weather conditions can influence energy expenditure during foraging and where food availability fluctuates with season (Grant 1995). Therefore, attempting to simulate the platypus's environment in the laboratory is difficult. However, the swim tank has profound advantages compared to more conventional methods used in the study of animal energetics. The method ensures both controlled experimental conditions and a good time resolution. Experiments with penguins (e.g. Culik and Wilson 1991, Culik and Wilson 1994, Kooyman and Ponganis 1994, Bethge et al. 1997) show that the swim canal method enables animals to voluntarily select their own swimming speed and dive duration while all activities and gaseous exchange can be closely monitored. In contrast, swim flumes (e.g. Baudinette and Gill 1985, Fish et al. 1997) force animals to dive or to retain a certain speed while swimming and consequently put them under unnatural conditions.

With the swim tank used in this study, it was possible to measure energy requirements during voluntary diving in platypuses. In addition, the design of the swim tank allowed the measurement of energy expenditure during foraging including food intake. Food was provided in the swim tank and was readily taken by the platypuses in a manner similar to that reported from the wild (Burrell 1927, Scheich et al. 1986, Kruuk 1993, Grant 1995). Therefore, results from the swim tank experiments are considered suitable to estimate energy consumption of platypuses foraging in the wild.

However, the limitations of the swim tank should be noted. Although voluntary behaviour was possible, the swim tank limited movements and diving patterns of the platypuses. Mean dive duration in the tank was 20 % shorter than in the wild. In addition, the number of dives performed per hour was much lower than during foraging in the natural habitat. Food was more easily available than in the wild and no energetically demanding searching be-

haviour or counter-current swimming was necessary. Therefore, we would expect that the energetic costs derived in a swim tank underestimate the power requirements of platypuses foraging in the wild.

4.4.2 Resting metabolic rates

The resting metabolic rate in air of the platypus derived in this study is consistent with that presented by Grant and Dawson (1978a) ($2.28 \text{ W kg}^{-0.75}$ at 26°C and $2.21 \text{ W kg}^{-0.75}$ at 25°C respectively). Similarly, the gradual increase in metabolism with decreasing temperature observed in this study is consistent with data recorded by Martin (1902), Smyth (1973) and Grant and Dawson (1978a). In this study, metabolism in air at 10°C increased to 1.5 times the resting level while immersion in water of 9°C raised the metabolism of the platypus to a maximum of 3.1 times RMR ($6.98 \text{ W kg}^{-0.75}$). Grant and Dawson (1978a) reported an increase in metabolism of 3.2 times RMR during immersion in water of 5°C and a maximum resting rate of $7.0 \text{ W kg}^{-0.75}$.

While resting metabolic rates in air were measured for fasted animals, resting metabolic rates in water were obtained from animals, which had access to food in the swim tank. An effect of feeding on the resting metabolic rates in water cannot be ruled out. However, MacArthur and Campbell (1994) reported that, in aquatic trials with muskrats, average steady-state oxygen consumption rates of fed animals were similar to values recorded from fasted animals, suggesting substitution of heat increment of feeding mainly for thermoregulatory heat production in semiaquatic species.

'Wedging' rates calculated in this study are well below the resting rates of platypuses on the water surface at similar temperatures. Although the body is totally submerged while 'wedging' and heat loss is expected to be higher than on the water surface, metabolism increased only to a maximum of 2 times RMR on land (4.1 W kg^{-1} at 9°C). This indicates a very effective mechanism of decreasing metabolism during 'wedging' and supports the work of Grant and Dawson (1978a) and Evans et al. (1994) who reported adaptations in the platy-

pus to greatly restrict heat loss and a profound bradycardia, especially in long dives of over one minute duration. Platypuses were observed 'wedging' under water in this study for up to 5 minutes.

Jones et al. (1987) reported 'wedging' in excess of 6 minutes in captive platypuses while Evans et al. (1994) recorded 'wedging' of up to 11 minutes duration. Evans et al. (1994) assumed that during inactive dives circulatory adjustments are made and blood flow to many tissues is restricted so that oxygen stores are saved for the heart and brain only. The authors reported that heart rate fell as low as 1.2 beats per minute in 'wedging' animals and concluded that dives of 3 to 4 minutes duration should be well within the capabilities of inactive animals. The reported physiological adaptations in combination with the low metabolic rate reported in this study could explain why platypuses are able to stay inactive under water for extended periods of time (see also Chapter 6.4.7).

Resting metabolic rates of monotremes are reportedly lower compared to those of marsupials and most eutherian animals (Dawson and Hulbert 1970, Grant and Dawson 1978a). However, in this study the platypus had a resting metabolic rate (RMR), which was only 4 % lower than that predicted for marsupials in general by Dawson and Hulbert (1970) and 33 % and 35% lower than that predicted for an eutherian mammal of similar size by Dawson and Hulbert (1970) and Kleiber (1932), respectively.

Irving (1973) proposed that semiaquatic and aquatic mammals have higher resting metabolic rates than terrestrial mammals to compensate for heat loss in water. Indeed, the metabolism of a number of semiaquatic species has been found to be considerably higher than that of terrestrial species of the same size (Morrison et al. 1974, Pfeiffer and Culik 1998, Borgwardt and Culik 1999). The results for the platypus are in line with these findings. RMR of the platypus was 165% and 132% higher than that of its terrestrial relatives, the long-beaked and the short-beaked echidna, respectively (Schmidt-Nielsen et al. 1966, Augee 1976, Dawson et al. 1979).

4.4.3 Metabolic rates for diving and foraging

Platypuses spend on average between 11 to 13 hours a day foraging (this study, see Chapter 6.3.2) hence diving and the costs involved are crucial to the platypus's energy budget. Fish et al. (1997) investigated the metabolism of swimming and diving in the platypus by measuring oxygen consumption in a recirculating water flume. The metabolic rate of their animals whilst swimming against a constant water current of 0.45 to 1.0 m s⁻¹ was 5.14 W kg^{-0.75} at a water temperature of 15°C (Fish et al. 1997). This is considerably lower than the rate for submerged swimming $P_{(DIVE)}$ derived in this study (7.34 W kg^{-0.75}). The difference can partly be explained by the fact that the rates derived in this study include the costs for the searching behaviour on the tank bottom. Surprisingly however, the active metabolic rate estimated by Fish et al. (1997) is 14 % lower than the resting metabolic rate of platypuses in water for a comparable water temperature determined by Grant and Dawson (1978a) (derived from graph: 6.0 W kg^{-0.75} at 15°C). This suggests that metabolic rates during swimming might have been underestimated by Fish et al. (1997). The low active rates determined by Fish et al. (1997) are also unexpected considering that animals in their study temporarily swam on the water surface, which is generally regarded as more costly for semiaquatic mammals (Williams 1989).

In contrast to the metabolic rate for submerged swimming $P_{(DIVE)}$, the foraging metabolic rate $P_{(FORAGE)}$ derived in this study includes the cost of diving to the bottom of the tank (phase-1-behaviour, see Chapter 3.3), the cost of their typical searching behaviour and food intake (phase-2) and the cost of resurfacing after the dive (phase-3). In the swim tank, animals were able to dive and forage voluntarily and displayed similar foraging behaviour to that observed in free-living individuals (Kruuk 1993). Therefore, the results presented here provide a good prediction of the minimal metabolic requirements of platypuses foraging in their natural habitat (see Chapter 4.3.2). However, for reason discussed earlier (Chapter 4.4.1), foraging rates measured in the swim tank are likely to underestimate power requirements of platypuses foraging in the wild.

As expected, foraging rates of the platypus were dependent on body mass and water temperature with low water temperatures resulting in higher rates and smaller individuals using more energy than larger animals, probably due to a higher surface to volume ratio (Schmidt-Nielsen 1984). In addition, foraging rates of the platypus were dependent on dive duration with short dives resulting in relatively higher foraging costs (see Chapter 4.3.2 and Fig. 4-3). Part of these higher costs may be explained by less metabolic depression in short dives. Evans et al. (1994) reported a marked bradycardia for platypuses while diving and found that heart rate fell in all dives, from pre-dive rates of 140-230 to 10-120 beats min^{-1} . However, heart rate fell less and was more erratic in shorter dives. Similarly, MacArthur and Karpan (1989) observed an increase in the extent of bradycardia with the period of submergence in muskrats. In addition, the observed increased energy consumption by platypuses making short dives can be explained by the high percentage of time spent on the costly descent. For example, in this study it was observed that in a 15 s dive platypuses spent nearly one fourth of their total foraging costs on the dive to the bottom of the tank. These results suggest that platypuses are likely to prefer shallow streams and pools for foraging and that they have a preference for longer dive durations, a view that is supported by observations from the wild. Only a low percentage of dives reported from the wild are shorter than 20 s (see Chapter 6.3.1 and Fig. 6-3, also Kruuk 1993, Evans et al. 1994). Ninety-eight percent of all dives recorded at Lake Lea went to depths of less than 3 m (Chapter 6.4.3).

4.4.4 Cost of transport for under water swimming

Cost of transport (COT, in $\text{J N}^{-1} \text{m}^{-1}$) is power [W kg^{-1}] divided by speed [m s^{-1}] and gravitational acceleration (9.81 m s^{-2}) and is the amount of energy required to transport 1 N over a distance of 1 m (Tucker 1970, Videler and Nolet 1990). COT was obtained from dives performed in the 3 meter long swim canal (n=119, from 12 animals). No food was supplied in the canal to minimise searching behaviour and to restrict behavioural activity to under water swimming only.

Cost of transport was derived following $COT = P_{(DIVE)} (v g)^{-1}$ where $v =$ speed [$m s^{-1}$], g is the gravitational acceleration and $P_{(DIVE)}$ is the power for subsurface swimming. Mean COT was $3.98 J N^{-1} m^{-1}$ ($SD=1.40$, $n=12$) and ranged from $1.85 J N^{-1} m^{-1}$ at $0.4 m/s$ to $5.88 J N^{-1} m^{-1}$ at $0.1 m/s$. Transport costs were significantly dependent on speed ($p<0.001$, see App. B-1) (Fig. 4-4). Data were divided in four speed classes ranging from 0.1 to $0.4 m/s$ for further analysis.

During swimming, power input first increases and then remains stable with rising speed (Hind and Gurney 1997, Videler and Nolet 1990). As swimming speed rises further, hydrodynamic drag, which increases roughly in proportion to the square of speed, becomes the predominant factor. The power to overcome hydrodynamic drag increases with the third power of speed (Schmidt-Nielsen 1995) which is why a third degree polynomial function was used to regress power input during subsurface swimming against speed (see for comparison Culik and Wilson 1994, Bethge et al. 1997, Borgwardt and Culik 1999) yielding $P_{(DIVE)} = 236.14 v^3 - 167.84 v^2 + 35.51 v + P_{(REST)[water]}$ where $v =$ swim speed and $P_{(REST)[water]} =$ power input during rest at the water surface ($4.81 W kg^{-1}$). The corresponding curve fit for cost of transport is

$$COT = 24.07 v^2 - 17.12 v + 3.62 + 0.49 v^{-1} \quad (n=4, r^2=0.90, \text{ Fig. 4-4}) \quad (4)$$

At the preferred swim speed of $0.2 m s^{-1}$ COT was $3.61 J N^{-1} m^{-1}$. However, to compare the platypus to other subsurface swimmers of different size, the minimum COT for the platypus was determined, which is a constant for each animal and can be used directly to assess the efficiency of different locomotor strategies (Taylor et al. 1970, Tucker 1970, Schmidt-Nielsen 1972, Videler and Nolet 1990, Fish 1992). Tucker (1970) defined an optimum swimming speed where the amount of work per metre reaches a minimum. Often, the lowest costs occur at the mid-range of routine speeds used by an animal and are within a trough of a U-shaped curve that relates transport cost to swimming speed (Williams et al. 1987, Williams 1989). Minimum COT for subsurface swimming platypuses derived from Equation (4) was $1.85 J N^{-1} m^{-1}$

(equals $18.12 \text{ J kg}^{-1} \text{ m}^{-1}$) at a swim speed of 0.40 m s^{-1} (Fig. 4-4). This speed is the optimal cruising speed for submerged swimming platypuses and is slightly slower than the optimum speed predicted by Videler and Nolet (1990) for a submerged swimmer with the body mass of a platypus (0.55 m s^{-1}).

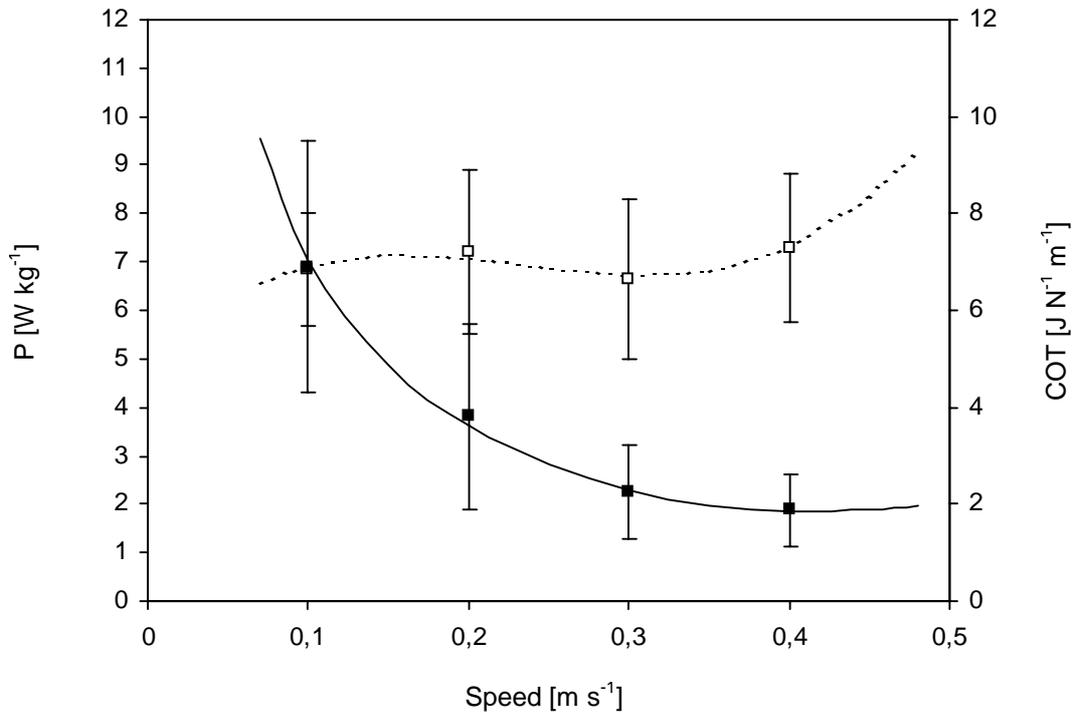


Fig. 4-4: Modelled cost of transport (solid line) and power input (dotted line) of platypuses swimming under water at various speeds in a swim canal, plotted as a function of swim speed. COT shows a minimum of $1.85 \text{ J N}^{-1} \text{ m}^{-1}$ at a swim speed of 0.4 m s^{-1} . Means \pm standard deviations shown.

Minimum COT derived in this study was three times higher than the minimum COT determined by Fish et al. (1997) (i.e. 0.51 at a speed of 1 m s^{-1}). For the reasons discussed above COT was probably underestimated in their study. In addition, Fish et al. (1997) did not observe a change in metabolic rate in the platypus over the speed range tested, which is rather unexpected for swimming animals (Videler and Nolet 1990, Hind and Gurney 1997). Also, the behavioural observations made in this study and a number of other studies (Evans et al. 1994, Manger and Pettigrew 1995) indicate that the swimming speeds chosen by Fish et al. (1997) (0.45 to 1.0 m s^{-1}) might have been far too

fast for normal platypus behaviour. Interestingly, platypuses in this captive study chose to swim at a mean speed of only 0.2 m s^{-1} , which is markedly slower than the optimal speed predicted (0.4 m s^{-1}). In addition, Otley et al. (2000) recorded radio tagged animals in the wild as swimming at speeds between 0.03 and 0.19 m s^{-1} while foraging. This suggests that platypuses rarely optimise for speed while foraging but rather spend their time performing a thorough search of an area. This finding is consistent with their observed feeding habits under water (Grant 1995).

4.4.5 Comparison with other mammalian swimmers

Costs for subsurface swimming in the platypus were found to be 51 % lower than predicted for a eutherian mammal of comparable body size (for comparison, data of MacArthur and Krause (1989), Williams (1989), Allers and Culik (1997) and Pfeiffer and Culik (1998) and were regressed against body mass, see Tab. 4-1). Muskrats for example (*Ondatra zibethicus*, body mass: 1 kg, MacArthur and Krause 1989) have an active metabolic rate nearly twice times as high as that of the platypus. Asian small-clawed otters (*Ambloonyx cinerea*, body mass: 3.1 kg, Borgwardt and Culik 1999) swimming under water expend energy at a rate 2.1 times that of the platypus. Also, resting rates of the platypus in air and water were found to be respectively 55 % and 56% lower than those predicted for its eutherian counterparts (Tab. 4-1). Thus, resting as well as submerged swimming platypuses appear to utilise energy at only half the rate of semiaquatic eutherians of comparable body size.

Surprisingly however, minimal transport costs of submerged swimming platypuses were similar to those obtained for semiaquatic eutherians, especially those obtained for otter species by Williams (1989), Pfeiffer and Culik (1998) and Borgwardt and Culik (1999) (Fig. 4-5). An allometric expression, $\text{COT} = 2.12 \text{ mass}^{-0.373}$ ($r^2=0.97$, $n=4$), was derived which describes the cost of transport for semiaquatic mammals ranging in size from 1.43 kg (platypus) to 19.9 kg (sea otter). Results obtained for the beaver by Allers and Culik (1997) however do not fit this allometric model.

	<i>Mass</i> [kg]	<i>RMR</i> [$W\ kg^{-1}$]	<i>Rest in Water</i> [$W\ kg^{-1}$]	<i>Subsurface swimming</i> [$W\ kg^{-1}$]	<i>Cost of Transport</i> (COT) [$J\ N^{-1}m^{-1}$]	<i>Swim Speed</i> [$m\ s^{-1}$]	<i>Locomotor Cost</i> (LC) [$J\ N^{-1}m^{-1}$]
Muskrat	1.0	4.39	N/A	12.49	N/A	N/A	N/A
ASC Otter	3.1	5.03	9.1	14.2	1.47	0.9	0.45
River Otter	6.2	4.1	6.4	12.1	0.95	1.3	0.45
Beaver	18.6	1.58	2.31	3.18	0.36	0.9	0.10
Sea Otter	19.9	3.72	4.58	5.95	0.76	0.8	0.18
Regression (for Eutherians)		$P_{(REST)AIR} =$ $-0.11 \times mass + 4.85$ $r^2 = 0.56$	$P_{(REST)WATER} =$ $-0.30 \times mass + 9.18$ $r^2 = 0.80$	$P_{(DIVE)} =$ $-0.51 \times mass + 14.51$ $r^2 = 0.89$			
Prediction for Platypus	1.43	4.69	8.75	13.79			
Platypus (this study)	1.43	2.08	3.91	6.71	1.85	0.4	0.85
Platypus/Prediction [%]		44	45	49			

Tab. 4-1: Energetic requirements of semiaquatic mammals during swimming and comparison to the platypus. Data on muskrats from MacArthur and Krause (1989), on Asian small clawed (ASC) otters from Borgwardt and Culik (1999), on river otters from Pfeiffer and Culik (1998), on beavers from Allers and Culik (1997), on sea otters from Morrison et al. (1974) and Williams (1989), on platypuses from this study.

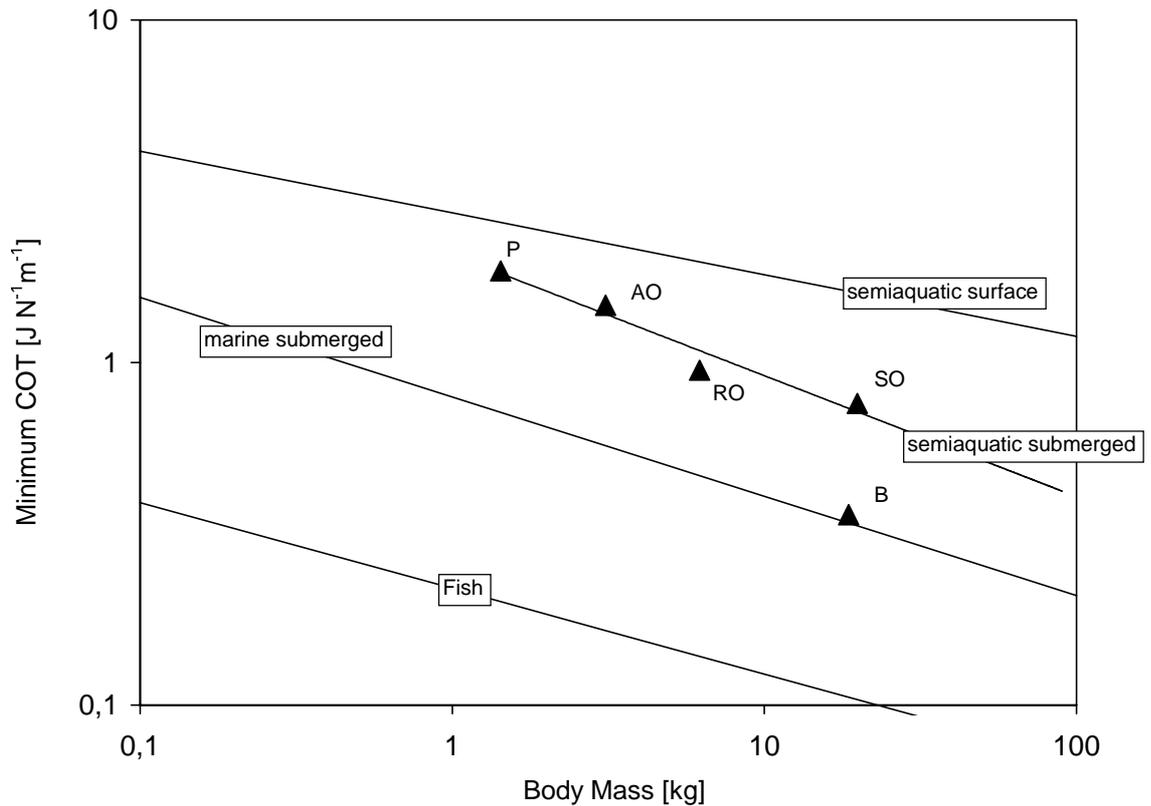


Fig. 4-5: Minimal transport costs of different semiaquatic swimmers (▲) plotted as a function of body mass (log/log plot). Submerged swimming data on Asian small-clawed otters (AO) from Borgwardt and Culik (1999), on river otters (RO) from Pfeiffer and Culik (1998), on sea otters (SO) from Williams (1989) and on beavers (B) from Allers and Culik (1997). Data on platypuses (P) from this study. Modelled transport costs in surface swimming semiaquatic mammals (Williams 1989), in marine mammals (Williams 1998) and in fish (Salmon) (Brett 1964) are shown for comparison. Model for COT in submerged swimming semiaquatic mammals (beaver excepted): $COT = 2.12 \text{ mass}^{-0.373}$.

Calculation of minimal cost of transport provides a common basis for comparing COT between animals of different size (Tucker 1970, Videler and Nolet 1990, Fish 1993a, Williams 1998). With this approach, locomotor energetics can be compared without consideration of velocity (Videler 1993). Transport costs can be described as the sum of maintenance costs (MC) and locomotor costs (LC) where MC is the cost for resting in water and LC is the energy expended for swimming performance (Williams 1989, Williams 1998).

Tab. 4-1 shows a comparison of locomotor costs (LC) for submerged swimming platypuses (this study) and eutherian semiaquatic animals. Locomotor costs of the platypus amount to 46 % of total COT. They are much higher than the relative locomotor costs of the other animals (Tab. 4-1). In effect, these high locomotor costs make up for the advantages the platypus experiences through lower maintenance costs.

The high locomotor costs of the platypus are likely to be a consequence of its small body size and the low under water swimming speed, which result in increased drag. Bannasch (1995) showed that for pygoscelid penguins friction drag is higher at low speeds or smaller body sizes. In addition, small animals do not seem to fit the allometric models (Culik and Wilson 1994, Williams 1998). In little penguins engaged in subsurface swimming for example, COT was twice as high as predicted (Bethge et al. 1997).

In addition, platypuses use a different swimming mode from otters. Like most other semiaquatic eutherians (also beaver *Castor canadensis*, muskrat *Ondatra zibethicus*), otters paddle with their hindlimbs in a vertical plane beneath the body (Fish 1993a). The platypus however uses pectoral rowing (Howell 1937, Grant 1989), a mode used by only a few other semiaquatic mammals including for example the ferret *Mustela putorius*. Both types of locomotion rely on drag based oscillating appendages, which provide thrust by entraining a large volume of water during stroke, a common morphological trend in semiaquatic mammals (Tarasoff 1974).

The most efficient paddle has the least streamlined shape and a large surface area (Barthels 1979), avoids drag interference with the body, and is triangular in shape which is the optimal shape for maximising thrust production during paddling (Blake 1981, Webb 1988). Examples include the appendages of river otters (Pfeiffer and Culik 1998), muskrats (Fish 1984) and sea otters (Williams 1989).

The propulsive forefeet of the platypus are also of triangular shape and constitute the largest surface area of any of the extremities. The combined surface area of the forefeet is 13.6 % of total body surface area (Grant and

Dawson 1978a). This is larger than the propulsive hindfeet of semiaquatic eutherians e.g. otters, which represent 4.0-6.4% of the wetted surface areas of the body (Mordvinov 1976). We would therefore expect the platypus to be the more efficient swimmer. However, this study suggests that the platypus's paddling mode might be less efficient than the hindlimb propulsion showed by the otter species.

Compared to animals with different strategies of locomotion in water, i.e. surface paddlers and specialised subsurface swimmers, the platypus, as expected, exhibits intermediate costs of locomotion (Fig. 4-5). COT determined in this study was 22 % lower than transport costs predicted from Williams (1989) for surface-swimming semiaquatic mammals ($COT = 2.73 M^{-0.18}$) but 149 % and 130 % higher than transport costs predicted by Culik and Wilson (1994) for subsurface-swimming homeotherms ($COT = 0.71 M^{-0.205}$) and by Williams (1998) for marine mammals ($COT = 0.79 M^{-0.29}$), respectively. The platypus has a COT 8 to 9 times greater than the minimum COT for a fish of equivalent body mass (Brett 1964, $COT = 0.22 M^{-0.25}$).

The higher rates for subsurface swimming in the platypus compared to more specialised divers can be explained by less specialisation for under water locomotion. The transitional lifestyle of the animal between two media sacrifices energetic efficiency for versatility and is likely to increase energy demands for locomotion on land as well as in the water when compared to specialists in one or the other environment. The platypus swims by pectoral rowing (Howell 1937, Grant 1989), which is considered inefficient. Only half the stroke of the limbs is used to generate forward propulsion (thrust), whereas the other half of the stroke, which is used to reposition the limb, increases the resistance to forward movement (drag), thus reducing the net thrust generated (Howell 1937, Fish 1984, Fish 1993a).

5 *Energetics of walking in the platypus*

5.1 Introduction

Terrestrial locomotion of mammals has been intensively investigated in the past (e.g. Taylor et al. 1970, Schmidt-Nielsen 1972, Taylor et al. 1982) and studies have produced surprisingly consistent results. Many mammals demonstrate predictable energetic and mechanical patterns during walking despite morphological differences. Typically for example, power requirements for walking in mammals increase linearly with increasing speed (Taylor et al. 1970) and can be expressed as a simple linear regression. Energy costs of locomotion for bipeds and quadrupeds have been found to be described by the same allometric equation regardless of size (Fedak and Seeherman 1979).

In contrast, there have been few studies on the energetics of walking in semiaquatic mammals, and it is not known whether or not their terrestrial locomotion follows the same patterns than that of specialised walkers. Studies on the Australian water rat *Hydromys chrysogaster* (Fish and Baudinette 1999) and on the mink *Mustela vison* (Williams 1983b) found elevated costs of walking compared to similar sized terrestrial mammals. Consistent with results for specialised walkers, power requirements increased linearly with increasing speed. The same was found to be true for the platypus (Fish et al. 2001). However, COT of the walking platypus was reported to be lower than transport costs of specialised walkers (Fish et al. 2001). This is surprising as the intermediate position of the platypus between terrestrial and aquatic specialists suggests higher costs for locomotion (Fish and Baudinette 1999).

The objective of this part of the study was to clarify the extent of physiological adaptation of the platypus to the terrestrial environment. The animal has a resting metabolic rate about one-half that found in placental mammals of the same body size and lifestyle (see Chapter 4). Also, its locomotory movement on land is unique and involves humeral long-axis rotation, horizontal retraction of humerus and femur and distally heavy limbs specialised for digging (Pridmore 1985).

5.2 Materials and methods

Rates for walking were obtained from eight platypuses (for details see Chapter 3.2). Experiments started on day three after capture. A conventional treadmill was used in conjunction with flow-through respirometry. A respiration chamber (Volume 28.3 l), constructed from transparent plastic sheeting, was placed on the treadmill for the experiments. The chamber was equipped with small wheels so that it could be fixed in a stable position while the treadmill was running. Oxygen consumption was measured using the open-circuit system described in Chapter 4.2.1. Data analysis followed the procedures outlined in Chapter 4.2.2. Data were only taken from animals walking constantly for at least 10 minutes.

5.3 Results

Platypuses would only walk on the treadmill over a narrow range of low walking speeds (0.2 to 0.3 m s⁻¹). At lower speeds, the animals tried to escape from the metabolic chamber. At higher speeds, they ceased walking in most cases and experiments had to be abandoned. The only gait used by the platypuses was walk. Metabolic rates $P_{(WALK)}$ were obtained from 8 animals and ranged between 8.80 W kg⁻¹ (at 0.2 m s⁻¹, SD=0.96, n=8) and 10.56 W kg⁻¹ (at 0.3 m s⁻¹, SD=0.93, n=8). Female platypuses used significantly more energy for walking than male animals (t-test, t=-2.23, p=0.034). Walking metabolic rates were regressed against speed and were significantly dependent on walking speed (p<0.001). Assuming a linear increase in metabolic rate with increasing speed for the platypus as demonstrated by Fish et al. (2001), walking metabolic rates for the platypus can be estimated following

$$P_{(WALK)} = 5.22 + 17.74 v \quad (n=16, r^2=0.82) \quad (5)$$

where v = walking speed [m s⁻¹] and $P_{(WALK)}$ = the metabolic rate for walking [W kg⁻¹].

5.4 Discussion

5.4.1 Metabolic rate and cost of transport for walking

Although mainly aquatic, platypuses are known to walk over land for extended periods of time (Photo 5-1), for example to get from one water body to the other (e.g. Otley et al. 2000), to circumnavigate dams or to avoid drought or flood conditions (Grant 1995). Consistent with results obtained for Australian water rats (Fish and Baudinette 1999) and mink (Williams 1983b), platypuses showed higher power requirements for walking than predicted for specialised walkers (Taylor et al. 1982). The slope of the derived formula for the walking platypus (Equation 5) is twice that predicted by Taylor et al. (1982) for a terrestrial mammal of similar size, i.e. 17.74 compared with a predicted value of 9.56 W kg^{-1} . Power requirements for walking at the observed speeds of 0.2 and 0.3 m s^{-1} were 19 % and 27 % higher than predicted.

Fish et al. (2001) reported walking metabolic rates for the platypus of 3.65 W kg^{-1} and 4.22 W kg^{-1} at speeds of 0.2 and 0.3 m s^{-1} , respectively. These rates amount to only half the rates measured in this study and are lower than those of similarly sized specialised walkers of eutherian origin (Taylor et al. 1982). Also, minimum transport costs for walking reported by Fish et al. (2001) were lower than those for specialised walkers (Taylor et al. 1982). These results are rather unexpected. The semiaquatic lifestyle of the platypus and a form of terrestrial locomotion, which is regarded as primitive (Pridmore 1985), suggest higher energetic costs for walking compared to locomotor specialists.

The platypus shows a unique locomotor movement on land, with humeral long-axis rotation, horizontal retraction of humerus and femur and distally heavy limbs specialised for digging. Limb orientations and limb movements of locomoting monotremes have been claimed to be essentially the same as those of lepidosaurian reptiles (Pridmore 1985). The short legs and the flattened body morphology produce problems of body support and restrictions in stride length not experienced by longer legged vertebrates. These limitations are likely to be

reflected in elevated energetic costs for walking compared to locomotor specialists and the results of this study confirm this suggestion.

Cost of transport of the walking platypus was derived following $COT = P_{(WALK)} (v g)^{-1}$ where $v = \text{speed [m s}^{-1}\text{]}$, g is the gravitational acceleration and $P_{(WALK)}$ is the metabolic rate for walking (Videler and Nolet 1990). COT ranged from 4.47 at a speed of 0.2 m s^{-1} to 3.58 at 0.3 m s^{-1} . The latter value is the minimum COT measured in this study. However, walking speeds of platypuses were very low on the treadmill. In the wild, the animal is likely to walk at higher speeds and will consequently have lower transport costs.



Photo 5-1: The walking platypus

The platypus differs from the majority of mammals in that its movement on land is restricted to symmetrical gaits. No other gaits have been reported for the animal, even at high speed walking in threat situations. It seems reasonable to assume that maximum walking speeds of the platypus do not extend to those speeds where animals of comparable lifestyle and body size change gait from symmetrical walk to faster gaits. Heglund and Taylor (1988) found that the

speed associated with gait transition could be predicted from body mass. For an animal of the mass of the platypus, the predicted speed was 1.7 m s^{-1} . This value is slightly higher than gait transition speeds found for mink (1.1 m s^{-1} , Williams 1983b) and Australian water rats (1.3 m s^{-1} , Fish and Baudinette 1999). Platypuses are not likely to attain speeds greater than this as the frequency of limb movement would get too high (Heglund and Taylor 1988) and gait transition does not occur.

The derived maximum walking speed of 1.7 m s^{-1} for the platypus allows an estimate of minimum transport costs to be made for comparison with other mammalian walkers yielding a minimum COT of $2.13 \text{ J N}^{-1} \text{ m}^{-1}$ for the walking platypus. Not surprisingly, this value is 30 % higher than minimum COT for the diving platypus indicating better locomotor adaptations for the aquatic than for the terrestrial environment.

5.4.2 Comparison with other mammalian walkers

Consistent with results for diving, the metabolic costs for walking were lower in the platypus than in eutherians with a comparable lifestyle and size. While mink (Williams 1983b) and Australian water rats (Fish and Baudinette 1999) show nearly similar power requirements for walking, platypuses expend energy at only half the rate. This finding is in line with results obtained for a terrestrial monotreme, the echidna. Edmeades and Baudinette (1975) found that total energy requirements for walking in the echidna was lower than in eutherians. The authors suggested that the low resting oxygen consumption of about one-half that found in placental mammals of the same body mass was responsible for this difference. The same can be said for the platypus. The generally low maintenance costs in monotremes seem to result in lower active metabolic rates compared to eutherians of comparable lifestyle and size.

However, minimum COT estimated for the walking platypus was slightly higher than results obtained for mink (Williams 1983b) and Australian water rat (Fish and Baudinette 1999) and shows the platypus to be the less efficient walker. Tab. 5-1 shows a comparison of locomotor costs (LC) for walking

platypuses (this study), mink (Williams 1983b) and Australian water rats (Fish and Baudinette 1999). Locomotor costs of the platypus amount to 93.9 % of total COT. They are relatively higher than locomotor costs of the eutherian animals (Tab. 5-1). In effect, these high locomotor costs make up for the advantages the platypus experiences through lower maintenance costs. Low running speeds and poor adaptations to the terrestrial environment are likely reasons for this inefficiency. Terrestrial mobility of semiaquatic animals has been found to correlate closely to the degree of aquatic specialisation (Tarasoff 1974). With increased specialisation of one locomotor mode, a subsequent reduction in locomotor agility of alternate modes occurs. Consequently, foraging is preferentially limited to a single habitat (Williams 1983a), which - in the case of the platypus - is clearly the aquatic environment.

	<i>Mass</i> [kg]	<i>Walking</i> [W kg ⁻¹]	<i>COT</i> [J N ⁻¹ m ⁻¹]	<i>Speed</i> [m s ⁻¹]	<i>LC</i> [J N ⁻¹ m ⁻¹]	<i>LC/COT</i> [%]
Platypus	1.43	5.22 + 17.74 v	2.13	1.66	1.99	93.9
Mink	0.94	13.4 + 11.26 v	1.51	1.78	1.30	86.2
Australian water rat	0.72	14.0 + 11.56 v	2.08	1.42	1.84	88.7

Tab. 5-1: Energetic requirements of semiaquatic mammals during walking and comparison to the platypus. Data on minks from Williams (1983b), on Australian water rats from Fish and Baudinette (1999) on platypuses from this study. v = speed in m s⁻¹.

6 Foraging behaviour and activity pattern of platypuses in a sub-alpine lake

6.1 Introduction

The platypus can be described as an opportunistic carnivore (Faragher et al. 1979) and is known to spend around half of its active time foraging for benthic invertebrates by diving and bottom searching in freshwater habitats around Australia (e.g. Grant 1983a, Grant 1995). Foraging ecology and activity pattern of the animal have been investigated in the past (Grant and Carrick 1978, Grant et al. 1992, Grigg et al. 1992, Serena 1994, Gust and Handasyde 1995, Otley et al. 2000). However, most studies on the behaviour of platypuses in the wild have involved populations occupying lowland river and stream systems on mainland Australia. Also, information on diving behaviour and foraging strategies of platypuses in the wild 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 ecology (Evans et al. 1994, Manger and Pettigrew 1995).

Foraging behaviour of the platypus 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). Radio-telemetry studies and body temperature measurements indicate a daily pattern of activity with the animals being largely, but not strictly, nocturnal (Grigg et al. 1992, McLeod 1993, Serena 1994). Increased variability in the time of emergence and in the incidence of diurnality was observed during the breeding season as well as during winter (Gust and Handasyde 1995, Otley et al. 2000).

Also, spatial and in some cases temporal separation of individuals was reported in a number of studies (Grant et al. 1992, Serena 1994, Gust and Handasyde 1995, Otley et al. 2000). This was suggested to be typical for carnivorous semiaquatic mammals that, like the platypus, occupy linear habitats (Gardner and Serena 1995). River otter and mink for example are known to display spatial systems in rivers similar to the platypus (Erlinge 1967, Gerrell

1970). In larger aquatic systems, a decrease in home range size and increased overlap of home ranges was observed for the platypus, which is a response shown by a number of mammals to increased population density (Sanderson 1966).

The objective of this part of the study was to elucidate diving behaviour and foraging strategies of platypuses in the wild and in particular in a lake system. Studies on platypus behaviour in lake habitats are sparse. Otley et al. (2000) investigated platypuses at Lake Lea (i.e. where this study was carried out) using radio-telemetry and suggested that the incidence of temporal separation and diurnal activity of platypuses was higher than in individuals in mainland studies. Differences in the distribution of prey, hydrology and physical characteristics of lake systems compared with river systems were suggested to result in different platypus behaviour.

This study aimed to further elucidate the dive cycles and seasonal foraging pattern of platypuses in the wild using data-loggers, a technique that has not previously been used in any studies on platypus ecology. Numerous studies to investigate foraging ecology of other diving animals were conducted using data-loggers. However, such research has been mostly limited to larger species in part due to their greater ability to carry such devices. With a mean body mass of only 1.78 kg (this study), the platypus is difficult to equip with systems to study behaviour in the wild. Yet, the method provides detailed information on a number of variables (including e.g. activity, dive duration, foraging rhythm and the time spent foraging and resting) in excellent time resolution and consequently allows the creation of a time-energy budget for the species (Costa 1988).

Such detailed observations of foraging and diving behaviour are particularly interesting in comparison with other semiaquatic mammals as they allow comparison between different diving strategies (Kramer 1988). Studies on otters show that observation on diving and foraging behaviour can be useful in the assessment of feeding and foraging efficiency of diving species in different habitats (Kruuk et al. 1990, Kruuk and Moorhouse 1991, Watt 1992).

6.2 Materials and methods

6.2.1 Experimental setup

Field experiments were carried out at Lake Lea, a sub-alpine lake in northwestern Tasmania (see Chapter 2.1 & 2.2 for site description and general methods). Foraging behaviour and activity pattern were successfully measured in 29 individual platypuses (17 adult males, mass: 2.10 ± 0.33 kg (SD), 10 adult females, mass 1.45 ± 0.11 kg (SD), and two subadults, see Tab. 6-1). 23 of the investigated individuals were assumed to be resident animals (i.e. at least one year between first and last catch) while six male individuals were assumed to be transient (i.e. less than one year between first and last catch).

None of the females equipped with data-loggers was lactating at the time of deployment. Data obtained from the two subadults (one male and one female, six to nine months of age) were analysed separately where appropriate. Individual details of the investigated platypuses are shown in Tab. 6-1 and Appendix A (together with the corresponding activity profiles obtained from data-loggers). Further details of the platypus population at Lake Lea are discussed in chapter 2.2.3.

Individuals were equipped with combined data-logger-transmitter packages (max 62 mm x 28 mm x 18 mm, weight 50 g, Photo 6-1, Photo 6-2) consisting of a specially designed standard transmitter (Faunatech, Eltham, Victoria, see App. C) and one of two types of data-loggers. Twenty-four individuals were successfully equipped with activity loggers (Actiwatch, Mini Mitter Co., Inc., USA, for details see Chapter 6.2.2) measuring activity and light in slow (AL) or fast (AL-F) sampling interval. Eleven platypuses were successfully equipped with time-depth recorders (TDR) which measured depth, ambient temperature and light (LTD_10, Lotek Inc., details see Chapter 6.2.2).

Data-logger-transmitter packages were bundled using fishing line and 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 in Serena (1994). Animals were then released at the site of capture.

After two days to six weeks depending on data-logger-type and sampling interval, the animals were relocated by radiotelemetry using a portable radio-receiver (Wildlife Telemetry Inc.) and a 3-element Yagi antenna. Animals were recaptured following the techniques described in Chapter 2.2.1 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.



Photo 6-1: Platypus equipped with data-logger-transmitter package

<i>Season</i>	<i>Identity</i>	<i>Sex</i>	<i>Age</i>	<i>Capture Date and Time</i>	<i>Recapture Date and Time</i>	<i>Trap Site I</i>	<i>Trap Site II</i>	<i>Weight I [kg]</i>	<i>Weight II [kg]</i>	<i>Logger Type</i>	<i>Status</i>	<i>Rhythm</i>	<i>Tag-No.</i>
Spring	10-98-1	m	adult	10.10.98 20:00	logger dropped	2	-	1.50	-	AL	transient	nocturnal	01C6-246B
	10-98-2	m	adult	19.10.98 22:40	logger dropped	6	-	1.82	-	AL	resident	mixed	01D2-D5DC
	10-98-3	m	adult	22.10.98 22:00	logger dropped	1	-	2.08	-	AL	transient	nocturnal	01D3-2F7F
	10-98-4	f	adult	24.10.98 22:50	11.12.98 22:00	1	10	1.46	1.48	AL	resident	mixed	01C6-38D5
Summer	12-98-1	f	adult	19.11.98 22:00	09.01.99 23:15	6	9	1.52	1.60	TDR	resident	mixed	0075-F749 *
	12-99-1	f	adult	10.12.99 00:15	04.01.00 22:00	6	3	1.54	1.56	TDR	resident	nocturnal	00F6-438A *
	12-99-2	m	adult	09.12.99 20:00	08.01.00 01:00	3	3	2.12	2.00	TDR	resident	nocturnal	0077-C753
	12-99-3	m	adult	09.12.99 23:00	05.01.00 20:00	3	3	2.00	1.94	AL	resident	mixed	01C5-OEAB
	12-99-4	m	adult	10.12.99 19:30	09.01.00 22:30	6	7	1.74	1.69	AL	resident	nocturnal	01F7-E8A9
	01-99-1	f	adult	06.01.99 23:20	06.02.99 00:00	6	6	1.42	1.42	AL	resident	nocturnal	0064-3898 *
	01-99-2	m	adult	08.01.99 23:25	26.02.99 23:15	1	11	2.17	2.21	AL	transient	mixed	0124-E365
	01-99-3	m	adult	12.01.99 18:00	25.02.99 22:05	3	9	2.20	2.28	AL	transient	mixed	01C6-D017
	01-99-4	m	adult	13.01.99 18:30	28.02.99 22:15	3	7	2.23	2.30	TDR	resident	mixed	0064-2E8F
	01-00-1	f	adult	05.01.00 21:20	22.01.00 21:00	3	3	1.49	1.40	TDR	resident	nocturnal	0075-F17E *
	01-00-3	m	adult	09.01.00 22:40	29.01.00 23:30	7	2	1.72	1.74	AL	resident	nocturnal	01D0-CCAD *
	01-00-4	m	adult	04.01.00 20:45	28.01.00 01:30	3	3	2.48	2.44	AL	resident	nocturnal	01C6-6FE2
	02-98-4	f	adult	16.02.98 08:30	16.03.98 01:15	6	6	1.43	1.34	AL	resident	nocturnal	0064-3898 *
	02-99-1	f	adult	28.02.99 22:00	18.03.99 13:20	7	12	1.46	1.36	TDR	resident	mixed	0075-F36D
	02-99-2	m	adult	28.02.99 22:00	19.03.99 19:30	7	7	2.14	2.06	TDR	resident	nocturnal	01F7-F0F0

Tab.6-1/1: Details of animals successfully used in field experiments (AL = activity logger, TDR = time-depth recorder, *individuals used more than once). See Appendix A for more information on individuals

<i>Season</i>	<i>Identity</i>	<i>Sex</i>	<i>Age</i>	<i>Capture</i> <i>Date and Time</i>	<i>Recapture</i> <i>Date and Time</i>	<i>Trap</i> <i>Site I</i>	<i>Trap</i> <i>Site II</i>	<i>Weight I</i> <i>[kg]</i>	<i>Weight II</i> <i>[kg]</i>	<i>Logger</i> <i>Type</i>	<i>Status</i>	<i>Rhythm</i>	<i>Tag-No.</i>
Autumn	03-98-1	m	adult	16.03.98 01:45	17.03.98 22:40	6	6	2.20	2.20	AL-F	transient	mixed	0064-6178 *
	03-98-4	m	adult	19.03.98 21:15	24.04.98 16:45	6	4	2.20	2.20	AL	transient	mixed	0064-6178 *
	03-98-5	f	adult	20.03.98 22:30	27.04.98 18:50	6	9	1.53	1.45	AL	resident	mixed	0075-F749 *
	04-98-1	f	adult	22.04.98 22:30	24.04.98 18:30	3	3	1.45	1.45	AL-F	resident	nocturnal	00F6-438A *
	04-98-2	f	adult	24.04.98 18:45	29.04.98 18:30	5	3	1.60	1.60	AL-F	resident	nocturnal	0075-FB2C *
	04-98-3	f	subadult	24.04.98 18:30	30.05.98 21:45	3	3	1.21	1.22	AL	resident	nocturnal	0075-F17E *
	04-98-4	m	subadult	29.04.98 06:35	02.06.98 23:15	9	9	1.56	1.53	AL	resident	nocturnal	01C6-11AC
	04-98-5	f	adult	29.04.98 18:30	31.05.98 18:30	5	3	1.60	1.44	AL	resident	nocturnal	0075-FB2C *
Winter	05-98-2	m	adult	02.06.98 09:05	13.07.98 14:00	3	3	2.72	2.47	AL	resident	mixed	0064-604D *
	05-98-3	f	adult	02.06.98 23:30	17.07.98 06:00	9	8	1.60	1.50	AL	resident	diurnal	0064-58E1
	06-99-1	f	adult	09.06.99 15:45	found dead	3	7	1.41	-	TDR	resident	diurnal	01C6-2F84
	06-99-2	m	adult	09.06.99 18:30	23.07.99 18:00	3	3	2.65	2.60	TDR	resident	mixed	0064-604D *
	06-99-3	f	adult	09.06.99 16:20	28.06.99 18:30	3	3	1.56	1.46	AL	resident	diurnal	00F6-438A *
	06-99-4	m	adult	09.06.99 18:50	found dead	3	3	2.07	-	AL	resident	nocturnal	0070-B623
	06-99-6	f	adult	09.06.99 21:30	logger dropped	3		1.54	-	TDR	resident	nocturnal	0075-FB2C *
	07-98-1	m	adult	12.07.98 15:45	29.08.98 19:30	3	3	1.96	1.90	AL	transient	mixed	0075-F6B7
	07-98-3	f	adult	18.07.98 06:30	27.08.98 20:00	2	2	1.47	1.38	AL	resident	nocturnal	01D1-F70D
	07-98-4	f	adult	18.07.98 20:30	29.08.98 23:35	6	6	1.16	1.09	AL	resident	nocturnal	00F6-3DCC
07-99-1	m	adult	01.07.99 20:00	27.11.99 00:00	2	2	2.62	2.60	AL	resident	nocturnal	0064-5E20	
07-99-2	m	adult	21.07.99 18:30	logger dropped	2	-	1.68	-	TDR	resident	nocturnal	01D0-CCAD *	

Tab. 6-1/2: Details of animals successfully used in field experiments (AL = activity logger, AL-F = activity logger with fast sampling interval, TDR = time-depth recorder, *individuals used more than once). See Appendix A for more information on individuals

Mean deployment time for the packages was 676 hours (28 days) and ranged from 44 hours to 1225 hours (51 days). Five animals dropped their packages after 28 to 45 days. Two animals were found dead with their packages still attached. Sixty percent of animals were recaptured at the same site where they were trapped the first time. All other animals were recaptured at a different site. There was no significant difference between the mean mass of the animals before and after the deployment period (t-test, $t=0.5$, $p>0.3$). Correspondingly, mean tail fat index did not change significantly over the deployment period (t-test, $t=-0.54$, $p>0.29$).

Overall, 51 experiments were attempted. Thirty-nine data sets were successfully retrieved (success-rate: 76%). From the individuals equipped with time-depth recorders (TDR), 11 data sets were downloaded (from six females and five males). In one case the data-logger failed and no data were retrieved. From the individuals equipped with activity loggers, 25 data sets (from 24 individuals, 15 males and 9 females) with slow sampling-interval (2 and 5 minutes) and three data sets (from two females and one male) with fast sampling-interval (2 sec) were successfully retrieved. In all other cases loggers malfunctioned mainly because of water leakage. Six individuals were equipped with both types of data-loggers (at different times) while one individual was equipped twice with an activity logger. The distribution of successful experiments over the year is shown in Tab. 6-2. Details of successfully deployed animals are shown in Tab. 6-1 and Appendix A.

<i>Season</i>	<i>No. of successful experiments (No. of individuals)</i>	<i>thereof with logger type:</i>		
		<i>AL</i>	<i>AL-F</i>	<i>TDR</i>
Spring	4 (4)	4 (4)	0 (0)	0 (0)
Summer	15 (10)	8 (7)	0 (0)	7 (7)
Autumn	8 (5)	5 (5)	3 (3)	0 (0)
Winter	12 (10)	8 (8)	0 (0)	4 (4)
Total	39 (29)	25 (24)	3 (3)	11 (11)

Tab. 6-2: Seasonal number of successful field experiments (number of individual platypuses in brackets). AL = activity logger, AL-F = activity logger with fast sampling interval, TDR = time-depth recorder

6.2.2 Data-logger details and data analysis

The time-depth recorders (LTD_10, Lotek Inc., Canada, see Appendix C) were of cylindrical shape with a drop nose to decrease drag (Length: 61.5 mm, \varnothing 18 mm, weight in air 16 g, see Appendix C and Photo 6-2). The devices allowed measurement of depth, ambient temperature and light levels with a data storage capability of one Megabyte (non-volatile FLASH memory). The depth rating of the devices was 20 metres. Pressure resolution was approximately 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).

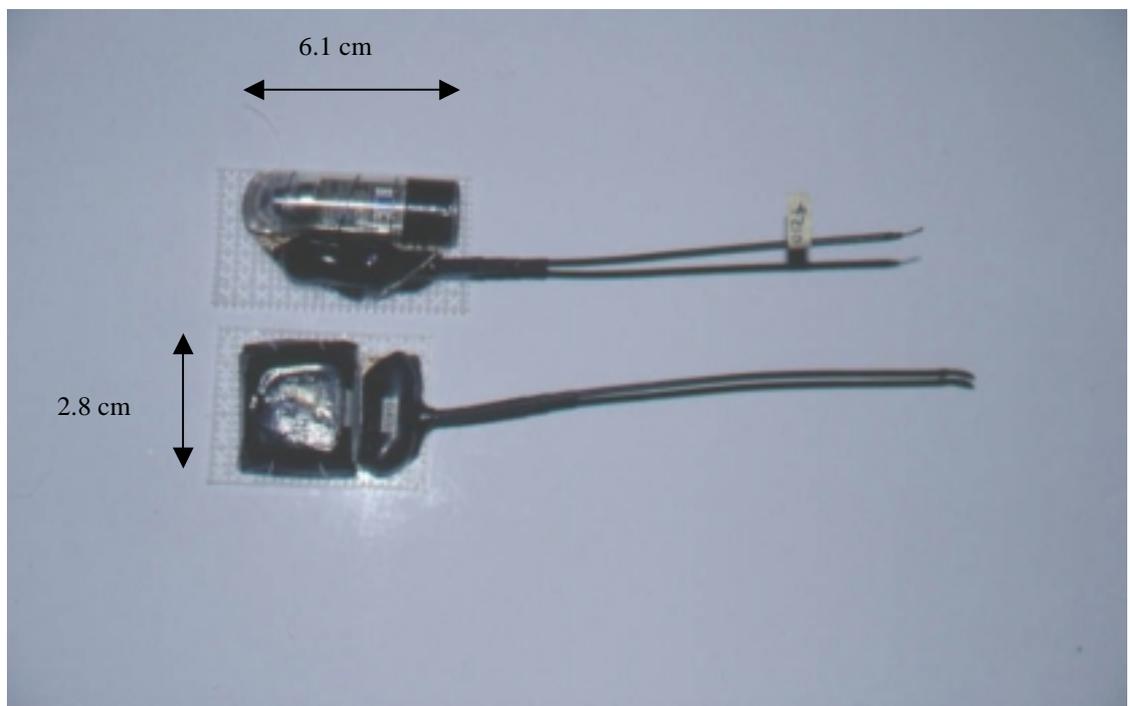


Photo 6-2: Data-logger packages used in this study. Top: Time-depth recorder, Bottom: Activity logger, combined with specially shaped radio-transmitter, respectively

The time-depth recorders were programmed to measure dive depth in two-second intervals and light intensity as well as ambient temperature in two-minute 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. 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, see App. C) was used. TDR-data were averaged over one-hour observation intervals. For each hour of foraging, light levels (night, twilight, day) as well as mean water and air temperature was derived. Data were then analysed in respect to the number of dives performed per hour, mean dive duration, mean surface duration and mean dive depth.

The activity loggers (Actiwatch, Mini Mitter Co., Inc., USA, see Appendix C and Photo 6-2) were square shaped (Size: 27 x 26 x 9 mm, weight 17 g) and allowed recording of activity and, in some cases, light levels into a 32 Kilo-byte on-board memory chip. Two types of devices were used; one equipped with activity sensor only (AW-3), the second type equipped with activity and light sensor (AW-L). Activity was measured with an accelerometer sensitive to <0.5 g integrating degree and intensity of motion. Values increase linearly with increasing activity, i.e. movement of the animal in any direction for any reason, but have no particular unit.

The devices were programmed to monitor activity (AW-3) or activity and light (AW-L) in two and five minute intervals. At these settings, recordings of up to 45 days were possible. After retrieval of the devices, data were downloaded using a specially designed reader and corresponding software (RhythmWatch, Mini Mitter Co., Inc., USA). This software was also used for graphic presentation of the data (Appendix A).

In addition, for calibration purposes (see Chapter 8.1) and to record diving activity in detail, the devices were run in two-second interval in some experiments. With these settings, recording time was limited to 18 hours only.

However, high-resolution activity data recordings were possible which allowed analysis of diving activity (see Chapter 6.3.1). Specially designed software (FastWatch, Mini Mitter Co., Inc., USA) was used to read these files.

Unfortunately, the activity loggers were not water-resistant and had to be sealed with a thin layer of waterproof epoxy-resin (Araldyte-M) before combining them with the radio-transmitters. This layer had to be removed each time the data-logger-battery had to be replaced.

Individual platypuses were tested multiple times in the experiments. To account for repeated measures, statistical tests were made using single factor or multiway factorial analysis of variance (ANOVA) with individual as a random factor and the effects in question as covariates. 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. Detailed statistical results for this chapter are summarised in Appendix B-2.

6.3 Results

6.3.1 Diving pattern

Using the time-depth recorders (TDR) a total of 98 foraging trips (1095 hours of foraging) from 11 platypuses (6 females, 5 males) were recorded during which 88906 dives were performed (see Tab. 6-1 & Tab. 6-3). Dive duration, descent, bottom and ascent duration, surface duration and maximum dive depth were derived. Dive depth in platypuses is directly dependent on water depth as animals usually dive to the bottom in search of food (e.g. Grant 1995). Sample data of diving activity is shown in Fig. 6-1.

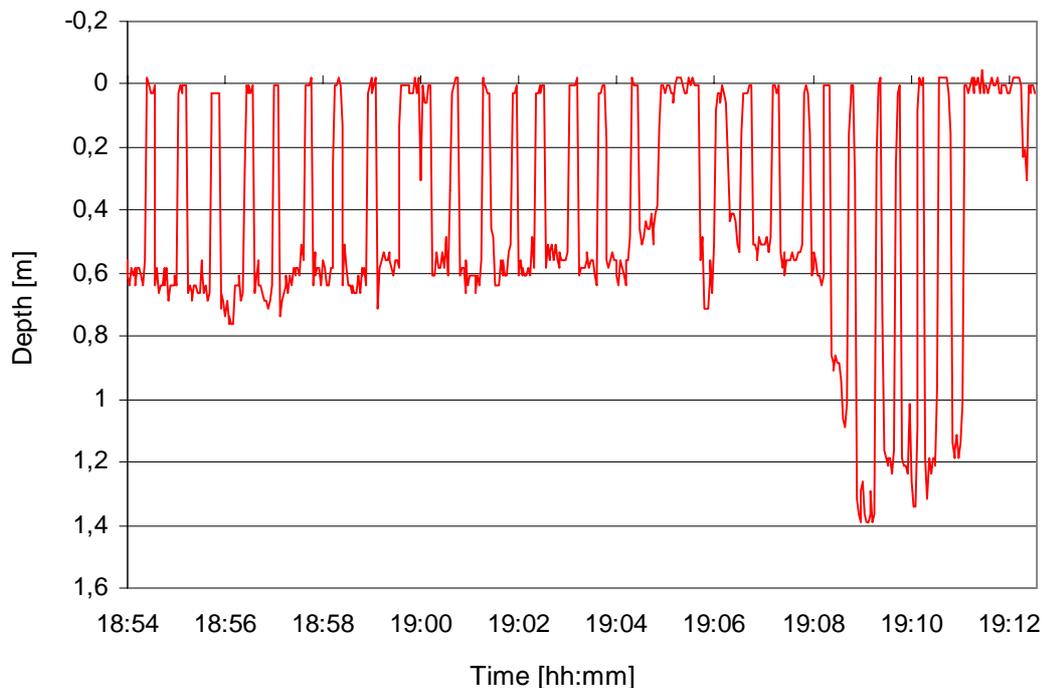


Fig. 6-1: Sample data of a female platypus (12-98-1) foraging at Lake Lea (derived from time-depth recorder, TDR)

For calibration purposes (see Chapter 8.1) three animals (one male, two females, see Tab. 6-1 & Tab. 6-3) were equipped with activity loggers (Actiwatch, Mini Mitter Co., Inc., USA) running with fast two-second sampling-interval (logger type: AL-F). These files showed subsequent bursts of activity which resembled diving activity recorded with the time-depth recorders (sam-

ple data see Fig. 6-2.). Consequently, these activity bursts were interpreted as dives. Thirty hours of diving activity of the three platypuses were recorded this way during which 1741 dives were performed. Data were analysed in respect to dive duration and inter-dive surface duration. Neither mean dive duration nor mean surface duration was significantly different between logger types (t-tests: $t=-1.217$, $P=0.221$ and $t=-1.893$, $p=0.058$, respectively). Therefore, data from both logger types were pooled for analysis.

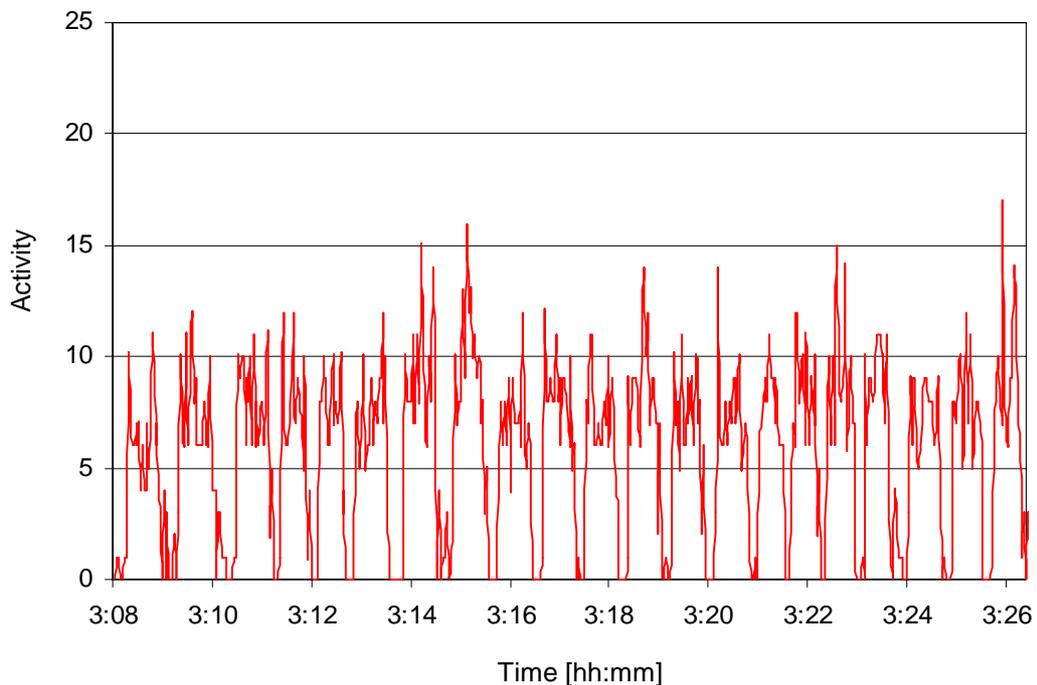


Fig. 6-2: Sample data of a female platypus (04-98-1) foraging at Lake Lea (derived from activity logger with two-second sampling interval; AL-F)

Dive duration of platypuses at Lake Lea averaged 31.3 s (SD=4.0, n=14) with 72 % of all dives ranging from 18 to 40 s (Fig. 6-3). Ninety-nine percent of all dives were less than 60 s long. 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 (SD=4.5, n=11). Descent duration, i.e. the time platypuses spend to dive from the surface to the lake bottom, averaged 3.9 s (SD=0.46, n=11) while mean ascent duration was 3.9 (SD=0.44, n=11). As-

suming a near vertical swim direction during descent and ascent, swim speeds for descent and ascent were determined by dividing dive depth versus descent and ascent duration, respectively. Descent swim speeds averaged 0.33 m s^{-1} ($\text{SD}=0.09$, $n=11$) while mean ascent swim speed was 0.32 m s^{-1} ($\text{SD}=0.09$, $n=11$). Both duration and swim speed did not vary significantly between descent and ascent (t-tests, $t=0.54$, $p=0.589$ and $t=0.82$, $p=0.437$, respectively). Maximum swim speed during descent/ascent was 3.0 m s^{-1} .

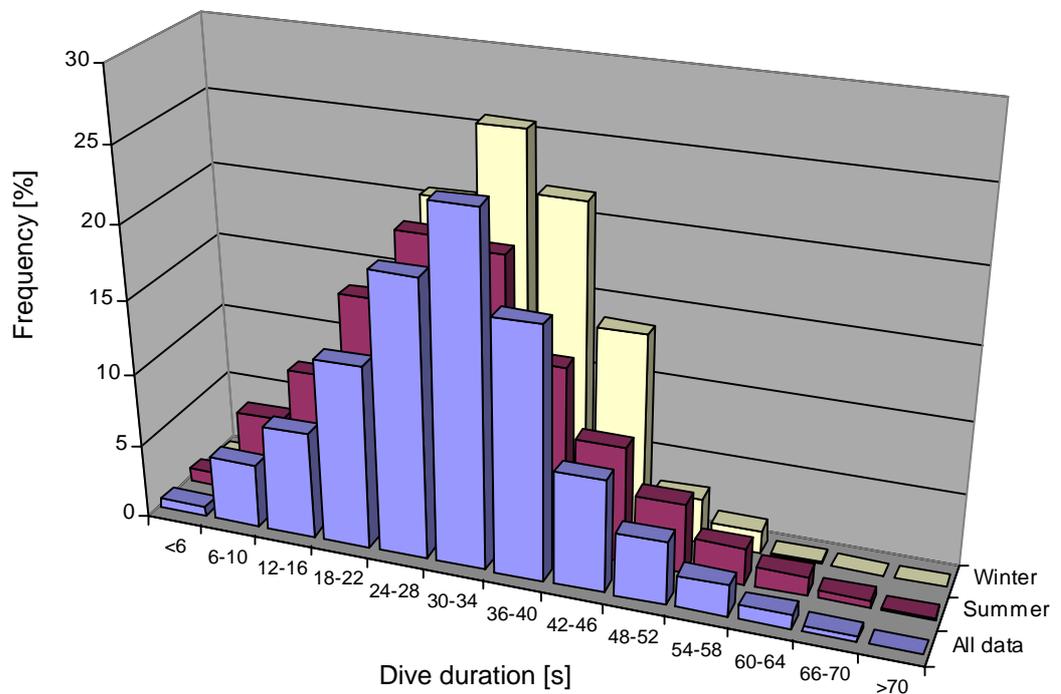


Fig. 6-3: Frequency diagram of platypus dive durations at Lake Lea (n=90647)

Mean surface duration between dives was 10.1 s ($\text{SD}=2.0$, $n=14$). Eighty-eight percent of all inter-dive surface durations lasted for less than 16 s (Fig. 6-4). Mean dive depth was 1.28 m ($\text{SD}=0.41$, $n=11$) with a maximum of 8.77 m. Ninety-eight percent of all recorded dives were not deeper than 3 m (Fig. 6-5). Results are summarised in Tab. 6-3.

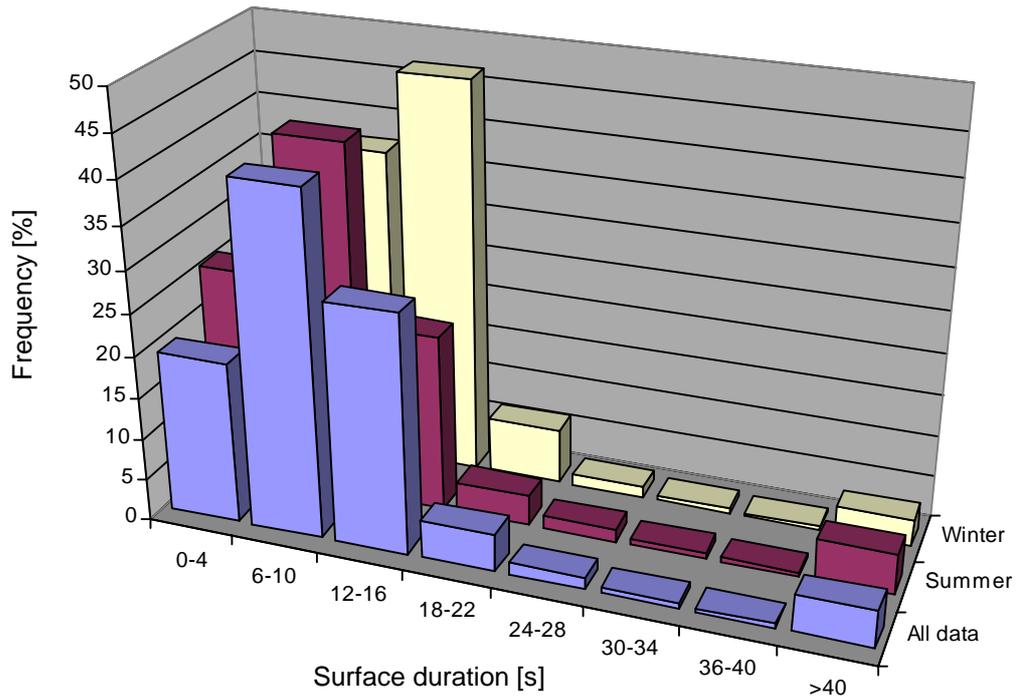


Fig. 6-4: Frequency diagram of platypus surface durations (n=90647)

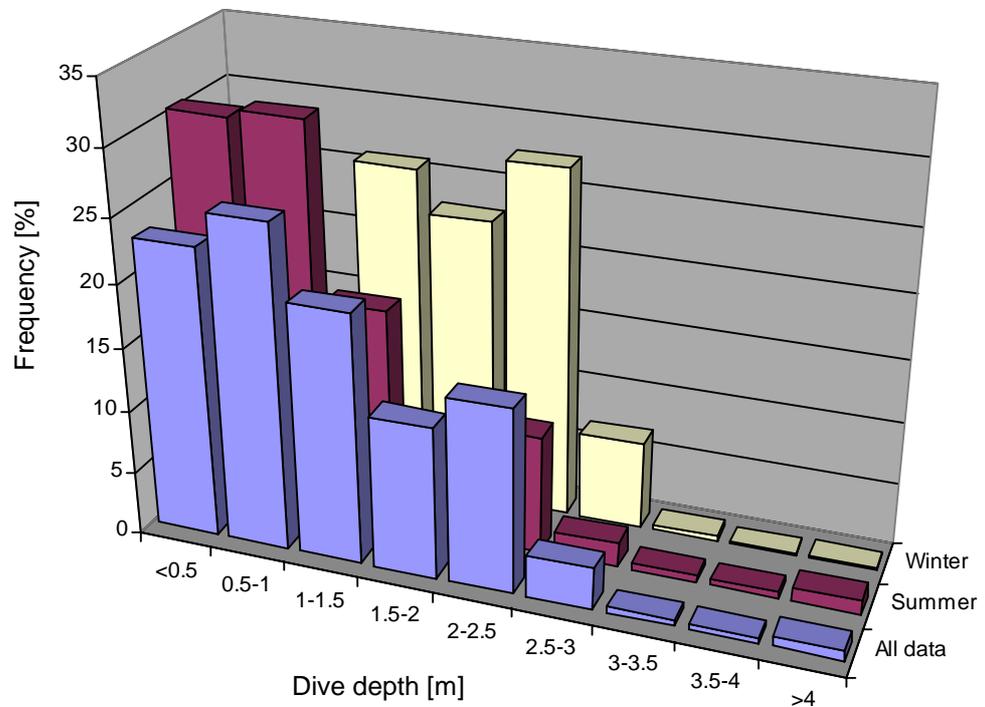


Fig. 6-5: Frequency diagram of platypus dive depths (n=88906)

Category	Identity	Sex	Logger type	Dive		Bottom		Surface		Dive Depth		n	Dive dur. / Surface dur. / Bottom dur. / Dive dur.	
				duration [s]	SD	duration [s]	SD	duration[s]	SD	[m]	SD			
Summer	12-98-1	F	TDR	27.8	(12.3)	20.3	(12.6)	8.3	(6.1)	1.05	(0.8)	12900	3.35	0.73
	12-99-1	F	TDR	23.1	(9.1)	15.7	(9.5)	8.4	(6.2)	0.86	(0.7)	12291	2.75	0.68
	12-99-2	M	TDR	33.0	(11.9)	24.7	(12.2)	10.1	(5.4)	1.26	(0.8)	10272	3.27	0.75
	01-99-1	M	TDR	35.3	(18.7)	27.5	(18.7)	10.3	(5.9)	1.40	(0.6)	5501	3.43	0.77
	01-00-1	F	TDR	24.4	(12.4)	14.9	(12.2)	6.4	(7.0)	0.95	(1.4)	9570	3.81	0.61
	02-99-1	F	TDR	30.6	(10.9)	23.5	(14.6)	10.5	(5.7)	1.13	(0.7)	3249	2.91	0.77
	02-99-2	M	TDR	30.4	(7.4)	23.7	(7.3)	10.3	(5.3)	0.84	(0.3)	9691	2.95	0.78
Autumn	03-98-1	M	AL-F	32.0	(8.3)			10.9	(7.3)	-	-	484	3.94	
	04-98-1	F	AL-F	30.4	(7.6)			11.6	(5.7)	-	-	803	2.72	
	04-98-2	F	AL-F	30.8	(10.8)			9.0	(7.6)	-	-	454	3.42	
Winter	06-99-1	F	TDR	30.8	(13.5)	23.4	(7.8)	10.1	(4.2)	1.25	(0.6)	3301	3.05	0.76
	06-99-2	M	TDR	36.9	(8.4)	28.1	(8.2)	13.6	(4.6)	2.04	(0.5)	5671	2.71	0.76
	06-99-6	F	TDR	32.9	(13.5)	23.5	(7.8)	10.2	(4.2)	1.26	(0.6)	8572	3.23	0.71
	07-99-2	M	TDR	37.0	(8.4)	28.2	(8.2)	13.7	(4.6)	2.02	(0.5)	7888	2.70	0.76
Means:														
Summer				29.2	(5.4)	21.7	(5.6)	9.2	(1.5)	1.07	(0.2)	7	3.17	0.74
Autumn				32.1	(0.3)			10.5	(1.7)			3	3.06	
Winter				34.4	(2.5)	25.3	(2.2)	11.9	(2.0)	1.64	(0.4)	4	2.89	0.74
Male				34.3	(2.6)	26.7	(3.4)	11.1	(2.1)	1.51	(0.5)	6	3.09	0.78
Female				29.1	(3.6)	20.6	(3.5)	9.3	(1.6)	1.08	(0.2)	8	3.13	0.71
Overall mean:				31.3	(4.0)	23.1	(4.5)	10.1	(2.0)	1.28	(0.4)	14	3.10	0.74

Tab. 6-3: Diving behaviour parameters of platypuses at Lake Lea (AL-F=activity logger, fast interval; TDR=time-depth recorder)

A significant correlation between dive duration and dive depth was found (ANOVA, $p < 0.001$, see App. B-2) and the relation is best described by the equation $\text{dive duration [s]} = 30.17 \text{ dive depth [m]}^{0.3001}$ ($r^2 = 0.96$, $n = 15$) (Fig. 6-6). In addition, a low but significant correlation between dive duration and subsequent surface duration was observed (ANOVA, $p < 0.001$, see App. B-2). This relation is best described by the equation $\text{surface duration [s]} = 0.16 \text{ dive duration [s]} + 4.89$ ($r^2 = 0.10$, $n = 90647$).

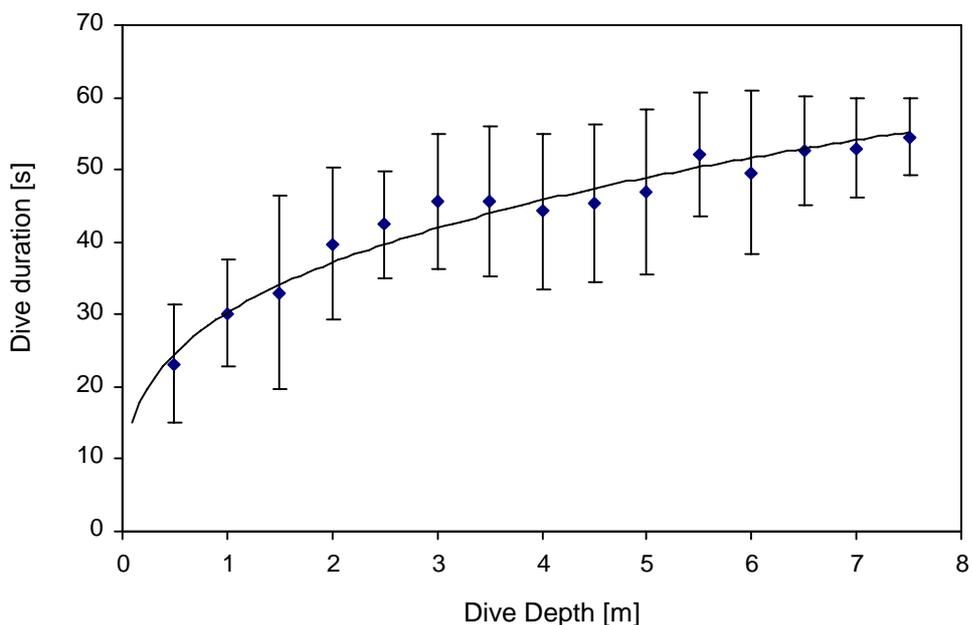


Fig. 6-6: The relationship between dive duration and dive depth of platypuses at Lake Lea. Bars show standard deviations. Regression: $\text{dive duration} = 30.17 \text{ dive depth}^{0.3001}$ ($r^2 = 0.96$, $n = 15$)

Mean dive duration, mean surface duration and mean dive depth was significantly different between the sexes and the seasons (two factor ANOVAs, $p < 0.05$ for any variable and both factors sex and season, see App. B-2). Both summer and winter data showed that male platypuses were diving significantly longer than female platypuses (t-test: $t = -2.943$, $p = 0.012$, $d.f. = 12$). Male platypuses were also diving significantly deeper than females (t-test: $t = -81.553$, $p < 0.001$, $d.f. = 12$) and spent significantly longer times on the water surface be-

tween dives (t-test: $t=-40.904$, $p=0.001$, $d.f.=12$). In addition, animals of both sexes were diving significantly longer and deeper in winter than in summer (t-tests: $t=-2.469$, $p=0.049$, $d.f.=9$ and $t=-2.933$, $p=0.017$, $d.f. = 9$, respectively). Also, surface duration was significantly longer in winter than in summer (t-test: $t=-2.536$, $p=0.032$, $d.f.=9$).

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, see App. B-2). In addition, the number of dives per hour was significantly dependent on season ($p<0.001$) as well as on sex of the platypuses ($p<0.001$) (three-factor ANOVA with additional factor light level, no cross-dependencies between factors, see App. B-2). Male platypuses dived significantly less often per hour than females but on average for longer. In winter (June, July August) platypuses of both sexes were diving significantly less often per hour but on average longer than in summer (December, January, February). On average, animals dived 75 times per hour ($SD=9.14$, $n=14$).

Light levels (night, twilight, day) were found to have a significant effect on dive duration ($p<0.001$), dive depth ($p<0.001$) and surface duration ($p=0.003$) as well as on the number of dives per hour ($p=0.003$) (three-factor ANOVAs with additional factors sex and season, see App. B-2). Platypuses dived longer and spent longer times on the surface between the dives at night. Correspondingly, the number of dives per hour was higher at daytime than at night. The highest number of dives per hour was observed at twilight. However, cross-dependencies between the factor light level and the factors sex and season were found for the variables dive duration, dive depth and surface duration (see App. B-2) and results have to be interpreted carefully.

Inter-dive surface durations of more than one minute duration were defined as resting periods or breaks during foraging. Analysis showed that platypuses, which were active during the day, performed fewer resting periods compared with those, which were active at night (t-test, $t=-3.696$, $p<0.001$).

Between 6 a.m. and 6 p.m., a break in foraging activity of more than one minute duration occurred on average after every 50th dive. Between 6 p.m. and 6 a.m. however, a comparable break in foraging already occurred on average after every 25th dive (Fig. 6-7). Overall, 61 percent of all breaks in foraging activity were between one and three minutes long. Only one percent of all breaks exceeded 10 minutes duration.

Dive/surface duration ratios averaged 3.17 respectively 2.89 for summer and winter animals and 3.09 respectively 3.13 for male and female platypuses. Mean dive/surface duration ratio at Lake Lea was 3.10. Bottom/dive duration ratios averaged 0.74 for both summer and winter animals and 0.78 respectively 0.71 for male and female platypuses (Tab. 6-3).

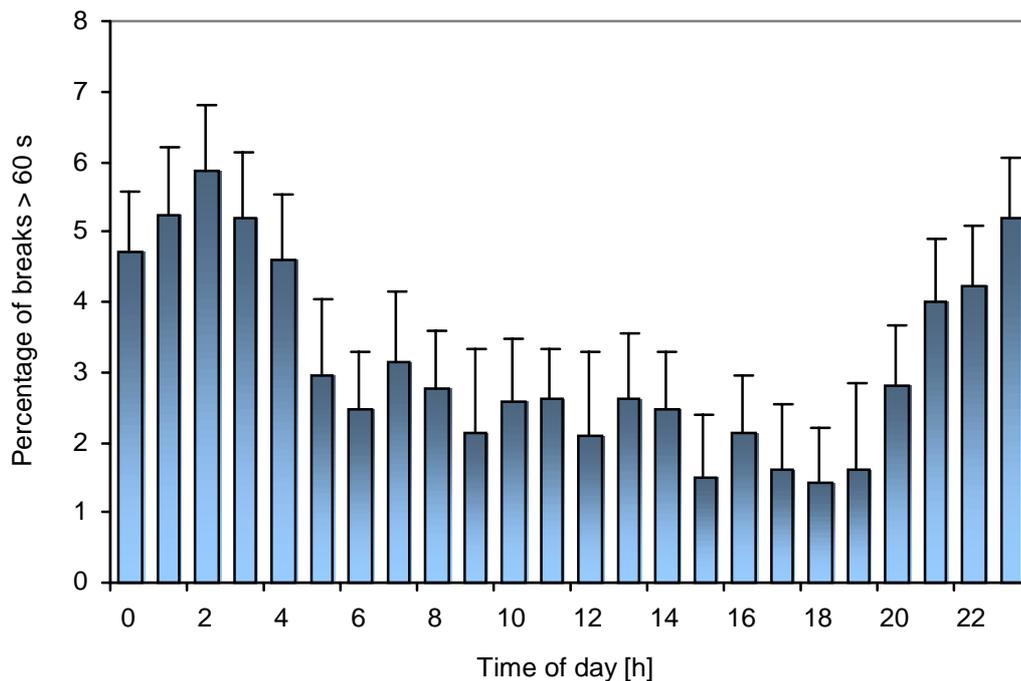


Fig. 6-7: Distribution of foraging breaks of platypuses at Lake Lea over the day, shown as percentage of all inter-dive surface durations (pooled data from 11 platypuses). Bars show standard deviation.

6.3.2 Activity pattern

Information on foraging pattern was obtained from 29 individual platypuses using both types of data-loggers. Activity profiles were recorded with the activity loggers for a total of 726 foraging trips (9950 hours of foraging) from 24 individual platypuses (15 males, 9 females, one female was used twice). Ninety-eight foraging trips (1095 hours of foraging) from 11 individual platypuses (six females, five males) were recorded using the time-depth recorders. For each foraging trip mean air and water temperatures as well as sun and moon rise and set times (from charts) were derived. Data from different logger types was analysed separately where necessary. Data from the two subadult animals did not deviate significantly from pooled data in most cases. However, some age-related differences in activity pattern were found which are discussed below. The recorded activity profiles are shown in Appendix A. For animal details see Appendix A and Tab. 6-1.

Foraging duration

The total period of activity (active period) was defined as the time span between activity onset and activity end. Only active periods of more than 30 minutes duration were used for analysis. The mean active period derived from activity loggers was 13.5 h day⁻¹ (SD=1.36, n=24) and ranged from 3.40 to 30.83 hours of continuous activity. The beginning of each active period was characterised by low activity levels for an average of 0.83 h (range: 0 to 3.25 h) followed by a sharp increase in activity. Correspondingly, at the end of each active period a sharp decrease in activity followed by low activity for an average of 0.35 h (range: 0 to 2.50 h) was observed.

Foraging duration was defined as the time span between the time of sharp activity increase and the time of sharp activity decrease. In 78 foraging trips, recorded light levels (indicating burrow exit) were used to estimate beginning and/or end of the foraging activity more accurately. The mean foraging

duration derived from the activity loggers was 12.4 h day⁻¹ (SD=1.14, n=24). Individuals performed foraging trips of up to 29.8 hours without resting.

Foraging duration measured by time-depth recorders 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 derived from the TDRs averaged 11.5 h day⁻¹ (SD=1.53, n=11) and ranged from 6.42 to 24.98 h of continuous foraging activity. The latter data were derived from one particular animal (01-99-4) which foraged on average twice as long as the other animals (details below).

Foraging duration measured both by TDRs and ALs was found to vary significantly according to season (AL: p<0.001, TDR: p=0.041) but not according to the sex of the platypuses (AL: p=0.233, TDR: p=0.227) (two-factor ANOVAs, see App. B-2). The same trends were observed for the active period (AL: season: p<0.001, sex: p=0.648, see App. B-2). On average, animals foraged (and were active) about one hour longer in winter than in summer (Tab. 6-4). However, foraging duration (measured both by TDRs and ALs) was not significantly influenced by water or air temperature (p>0.05 in all cases, see App. B-2). Seasonal foraging durations and active periods of platypuses at Lake Lea are summarised in Tab. 6-4.

	<i>Device</i>	<i>Spring</i>	<i>Summer</i>	<i>Autumn</i>	<i>Winter</i>	<i>Average</i>
Foraging duration [h day ⁻¹]	TDR		11.17		12.18	11.50
	AL	12.38	11.88	12.47	13.15	12.40
Active period [h day ⁻¹]	AL	13.72	12.95	14.07	14.20	13.51

Tab. 6-4: Mean seasonal foraging durations and active periods of platypuses at Lake Lea

Foraging pattern

Typically, all platypuses began foraging immediately after leaving the burrow and foraged continuously over the whole duration of the foraging trip. However, foraging patterns were dependent on a number of factors including

water and air temperatures, season, sex of the platypus, light levels and relative time of foraging trip. The mean number of dives per foraging trip measured with the time-depth recorders was 850 (SD=121.8, n=11). Individuals performed up to 1589 dives per foraging trip. Mean activity per foraging trip derived from the activity loggers was 263576 (range: 58151 to 551925, no unit). Mean daily activity was 266426 (range: 73485 to 514524). Daily activity was defined as the total activity over each 24-hour period from noon to noon.

Daily activity of platypuses at Lake Lea was dependent on season. Significant differences in activity between the months were observed (ANOVA, $p < 0.001$, and Tukey test, see App. B-2). Daily activity was highest from August to November and lowest in January (Fig. 6-8).

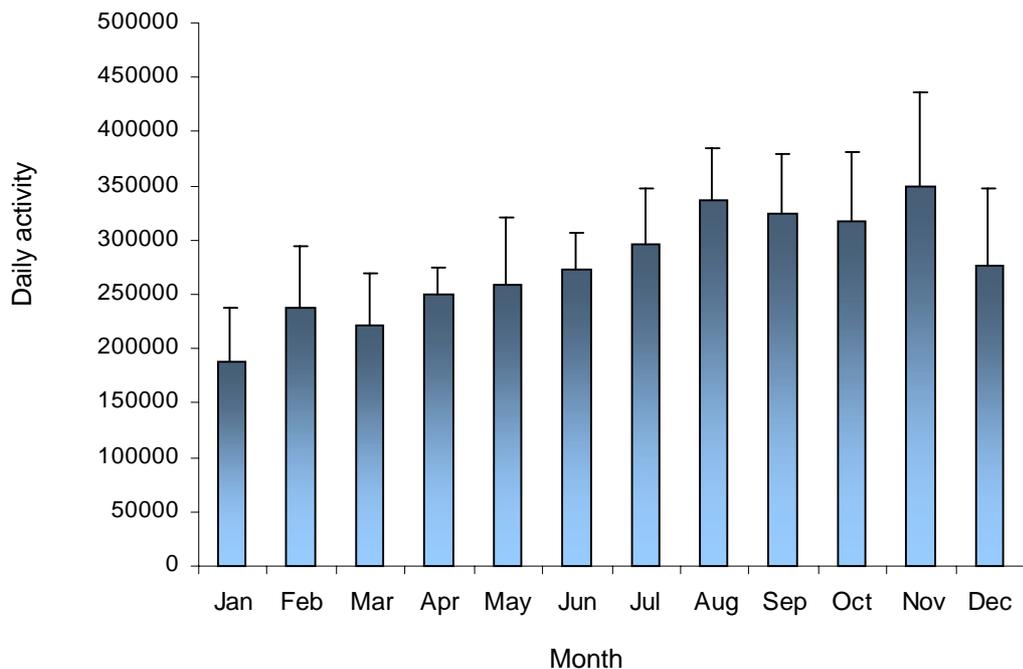


Fig. 6-8: Daily activity over the year of platypuses at Lake Lea. Bars show standard deviations

Correspondingly, the degree of daily activity was significantly dependent on water temperature ($r^2=0.195$, $p < 0.001$). Lower water temperatures caused higher daily activity (Fig. 6-9). However, no effect of air temperature on daily

activity was observed ($p=0.866$, see App. B-2). Also, the sex of the platypuses had no significant influence on the degree of daily activity (ANOVA, $p=0.362$, see App. B-2).

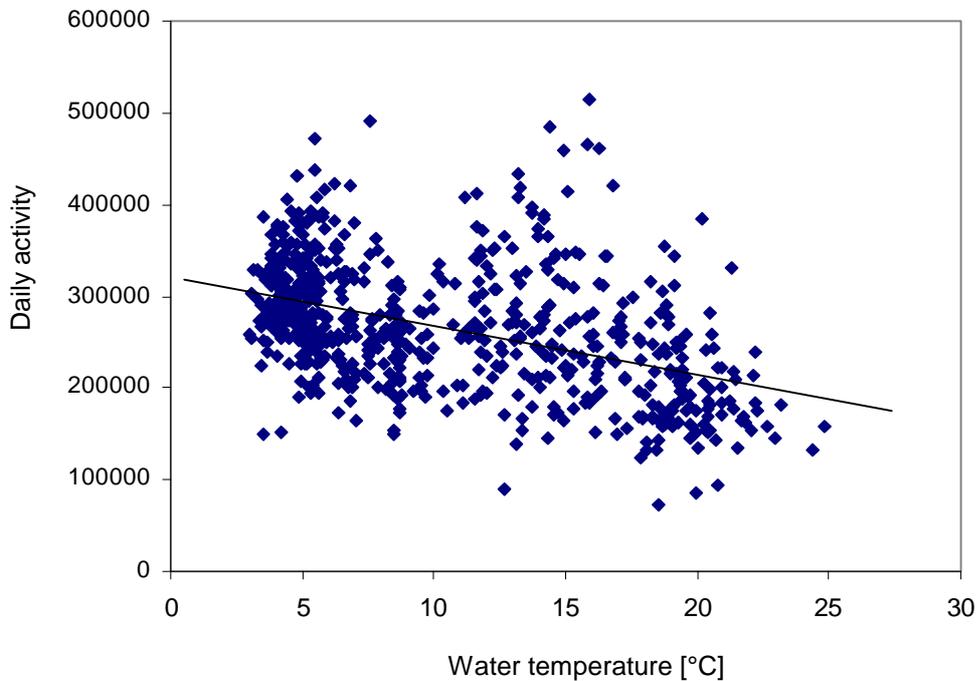


Fig. 6-9: The relation between daily activity and water temperature in platypuses at Lake Lea. Solid line shows regression ($r^2=0.195$, $n=726$).

Foraging trips were then divided to 10 time segments of equal length. For each time segment the total activity was derived and expressed as percentage of total daily activity. Statistical analysis of pooled activity data (Fig. 6-10) showed significant time-dependant changes in activity over the time of foraging. (ANOVA, $p<0.001$, see App. B-2). Pairwise comparison (Tukey-Test, see App. B-2) revealed that time segments two to six formed a homogenous group with no significant differences in activity levels between each other. Time segments one and 10, however, (i.e. beginning and end of the foraging trip) showed activity levels, which were significantly higher than all other activity levels. In addition, activity towards the end of the foraging trip (time segment 10) was significantly higher than at the beginning of the trip (time segment one).

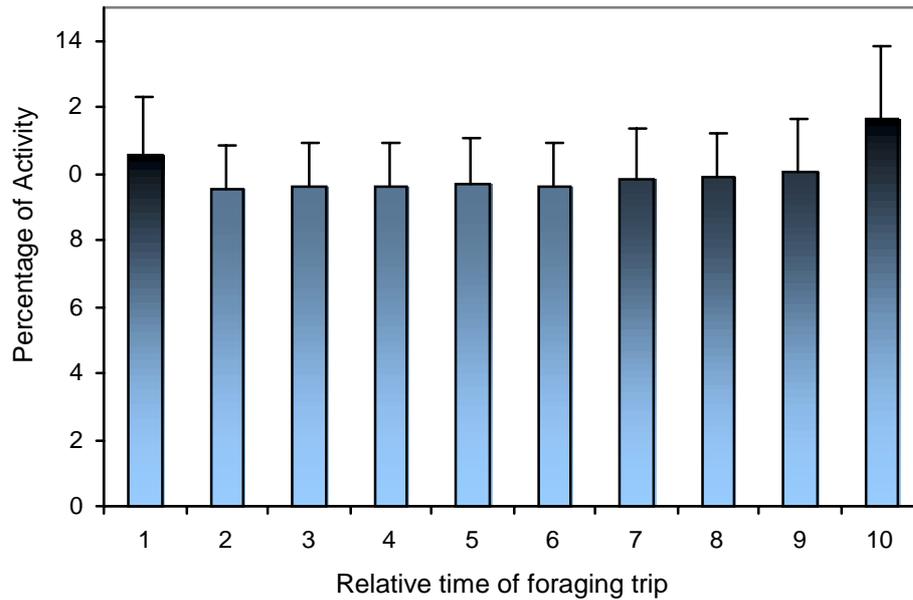


Fig. 6-10: Distribution of activity over the time of foraging in platypuses at Lake Lea (pooled data from 24 platypuses). Bars show standard deviations

Temporal activity pattern

Data from both logger types were grouped into nocturnal, diurnal and ‘mixed’ activity patterns. A foraging trip was regarded as nocturnal if 80 percent of the trip was performed during nighttime (from 6 p.m. to 6 a.m.). Accordingly, a foraging trip was regarded as diurnal if 80 percent of the trip was performed during daytime (from 6 a.m. to 6 p.m.). All other trips were regarded as ‘mixed’. To calculate circadian periods, the circadian physiology software package provided by Refinetti (2000) was used.

Sixty-one percent of all foraging trips were nocturnal while 31 % were ‘mixed’ and 8 % were diurnal. Nocturnal activity was highest in summer and autumn while diurnal activity occurred predominantly in the winter months (Fig. 6-11). Diurnal activity was mainly observed in female platypuses and was rare in male individuals. Females showed diurnal activity in 16 % of all foraging trips while males were diurnal in 2 % of all trips (Fig. 6-12). Strictly diur-

nal behaviour over a number of consecutive days was only observed in winter in three adult female individuals (05-98-3, 06-99-3 & 06-99-1).

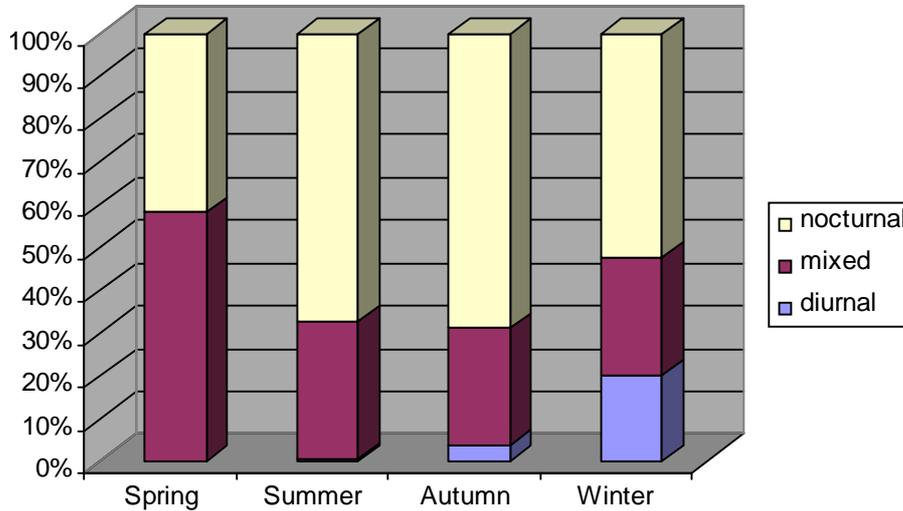


Fig. 6-11: Seasonal activity pattern of platypuses at Lake Lea (pooled data from 824 foraging trips of 29 individuals)

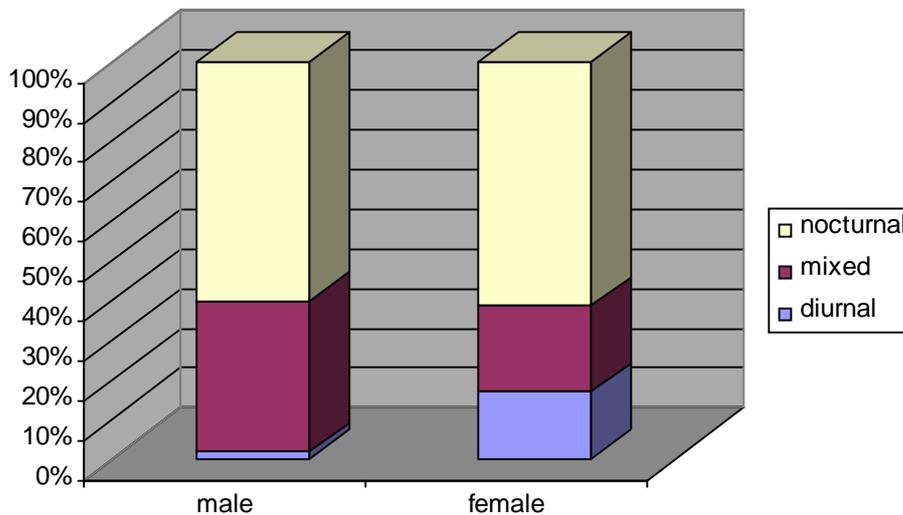


Fig. 6-12: Activity pattern of male and female platypuses at Lake Lea (pooled data from 824 foraging trips of 29 individuals; 18 males, 11 females)

The percentage of hours spent foraging during the day (6 a.m. to 6 p.m.) ranged from 17 % in summer and 21 % in both spring and autumn through to a maximum of 33 % in winter (Fig. 6-13). However, the percentage of foraging hours spent under light conditions (changing with season due to day length) did not vary that much over the year and ranged from 26 % in both spring and summer through to 19 and 21 % in autumn and winter, respectively (Fig. 6-14).

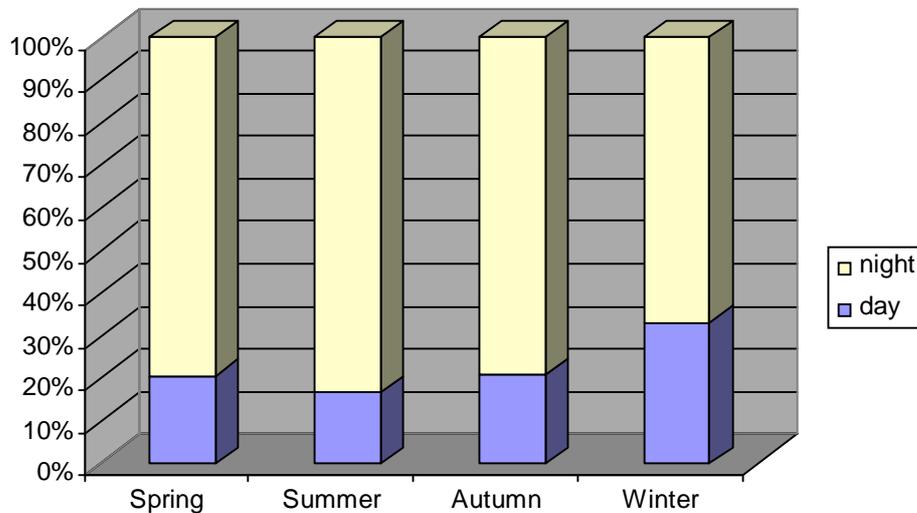


Fig. 6-13: Percentage of foraging hours spent over the day (6 a.m. to 6 p.m.) and during nighttime (6 p.m. to 6 a.m.) over the year (pooled data from 824 foraging trips of 29 individuals). See for comparison Fig. 6-14.

Long term observations between five to 48 days were obtained from 36 experiments using 29 individuals (see Appendix A). All animals investigated in this study clearly followed a circadian rhythm. The chi-square test was used to estimate circadian periods (chi-square-periodogram, Sokolove and Bushnell 1978, Refinetti 2000). Circadian periods ranged from 23.7 to 24.1 h and from 23.4 to 24.1 h in AL- and TDR-data, respectively. The six transient platypuses did not show a different distribution of activity pattern compared to the resident platypus population. Three transient males were found to be nocturnal while the other three showed 'mixed' activity.

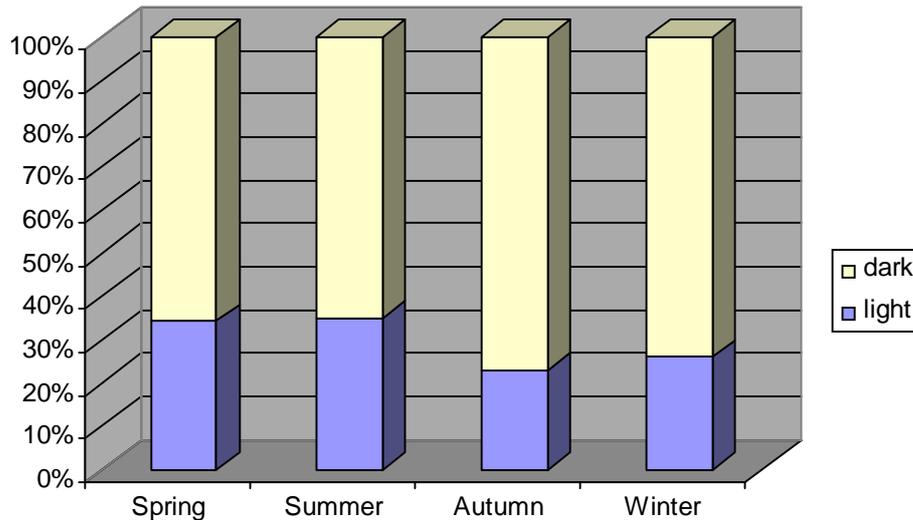


Fig. 6-14: Percentage of foraging hours spent in the dark and during daylight hours over the year (pooled data from 824 foraging trips of 29 individuals)

Emergence and return times of nocturnal and diurnal animals deviated up to six hours from sunrise/sunset times and changed slightly from day to day in most animals. However, 53 % of all platypuses with nocturnal or diurnal rhythm emerged and returned within one hour before/after sunset/sunrise times (Fig. 6-15). Accordingly, a low but significant correlation between sunset/sunrise times and the corresponding emergence/return times in nocturnal and diurnal animals was found ($r^2=0.082$, $SE=1.63$ h, $p<0.001$ and $r^2=0.033$, $SE=1.66$ h, $p<0.001$, sunrise and sunset times, respectively). There was a preference to emerge/return in the dark (58 % of all emergence/return times) rather than in daylight (42 %) (Fig. 6-15). However, in pooled data (including platypuses with ‘mixed’ behaviour), no correlation between sunset/sunrise and emergence/return times was found ($p>0.05$).

Nocturnal as well as diurnal platypuses showed a surprisingly high variability in behaviour. Quite regularly, individuals changed start and end time of their active period within days. Seemingly erratic changes in emergence and return times of up to a couple of hours as well as substantial changes in foraging trip length from day to day were obvious (see Appendix A).

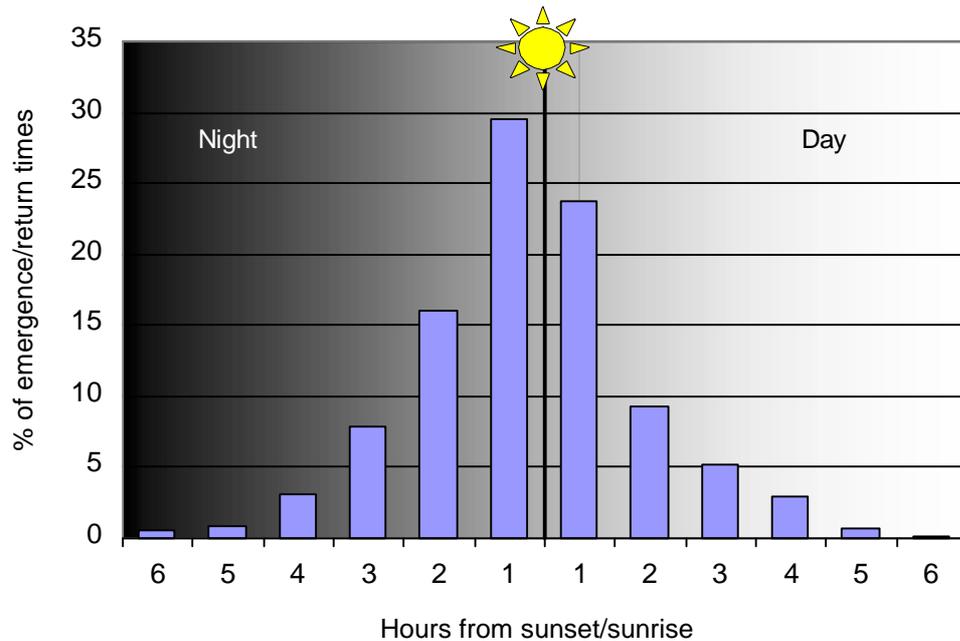


Fig. 6-15: Deviation of emergence and return times of nocturnal and diurnal platypuses from sunset/sunrise times (n=1139)

Animals grouped into the activity pattern category 'mixed' showed behaviour that was even more erratic. In three animals (10-98-2, 01-99-2 & 03-98-5, see Appendix A), foraging activity was found to be relatively regular, interrupted by very long foraging trips of up to 30.8 h (01-99-2). One platypus (01-99-4) showed a distinct 24-hour rhythm where 24-hour-foraging trips alternated with 24-hour-resting periods. Although only seven days of activity were recorded, the animal still followed the same rhythm when it was recaptured another six days later. The most irregular behaviour was shown by a female animal (10-98-4), which lived at Bonds Creek (Site 1, see Fig. 2-3) and which was recaptured in a little pool in the Vale of Belvoir. Very erratic changes in emergence and return times as well as in foraging trip duration were observed.

In contrast, emergence and return times of the two subadults (female 04-98-3 & male 04-98-4, see Appendix A) examined in autumn 1998 were much more regular than those of the adult platypuses. Both platypuses were strictly nocturnal. One of the subadults (female 04-98-3) was equipped with a TDR in

the summer nearly two years later (01-00-1). Now an adult, the animal was still nocturnal and used the same burrow area but showed a much more variable activity pattern with emergence and return times changing by up to five hours from day to day.

Two platypuses (03-98-4, Fig. 6-16 & 12-98-1, Fig. 6-17) clearly followed a lunar rhythm in their foraging pattern with both full and new moon possibly causing a change in behaviour. Both animals synchronised their activity pattern with moon rise and set times. At full or new moon, respectively, they slowly shift their active period back by one lunar rhythm only to synchronise their behaviour again with the moon at the next new and full moon, respectively.

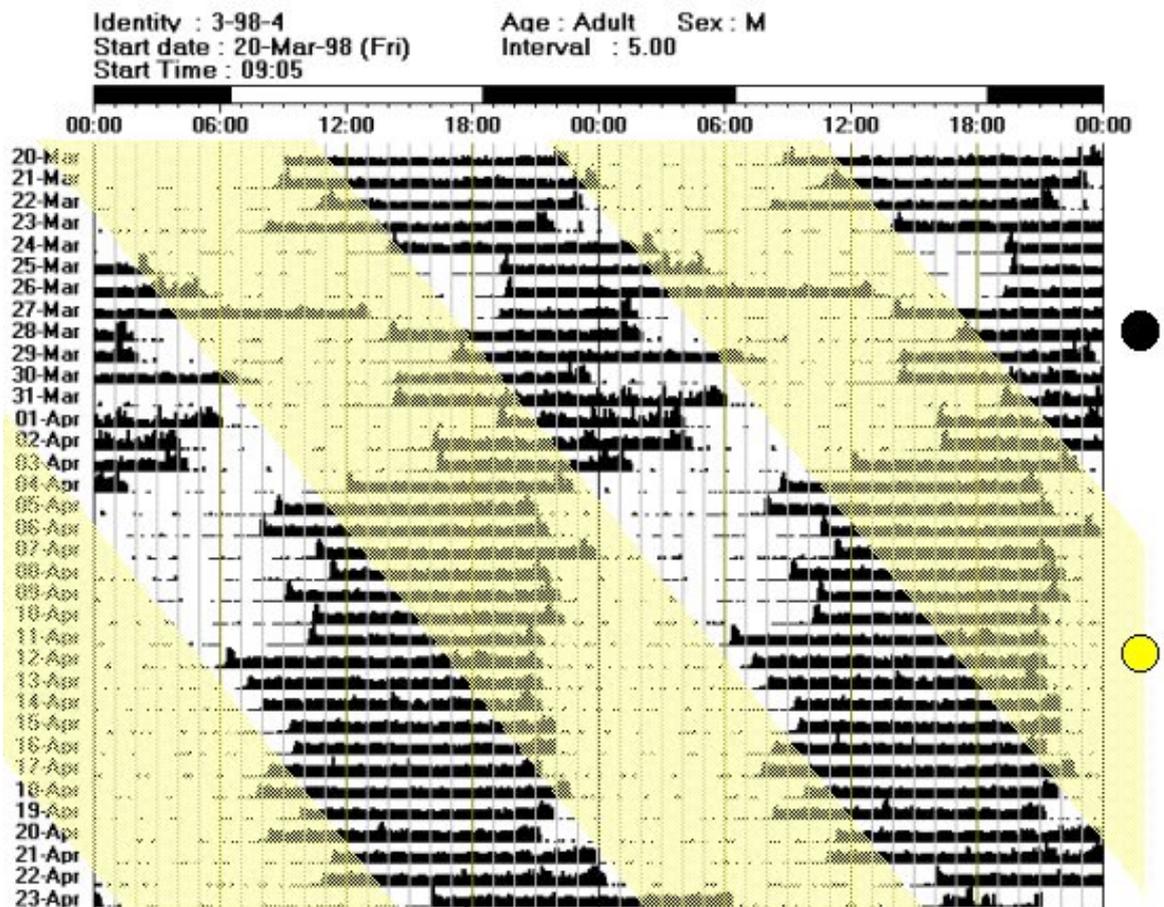


Fig. 6-16: Sample actogram of a male platypus (03-98-4) showing a lunar activity rhythm. Shaded areas show moonlight hours. Circles show new (closed circle) and full moon (open circle). Explanation see text

While the male platypus (03-98-4) chose to be active preferentially without moonlight (between moonset and moonrise times), the female platypus (12-98-1) chose to swim during moonlight hours. Two more platypuses (02-99-1 & 12-99-3) are likely to have been following lunar rhythms. However, observation periods in these animals were too short to confirm this suggestion.

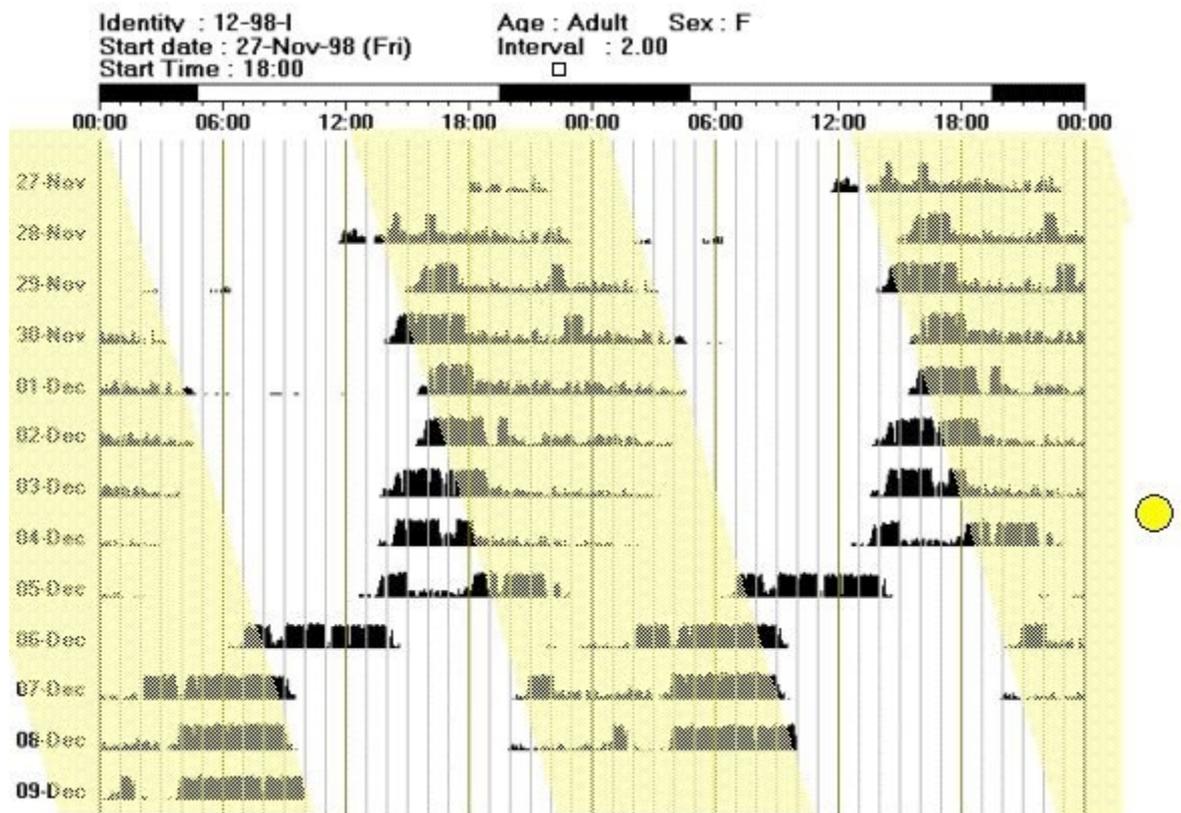


Fig. 6-17: Sample actogram of a female platypus (12-98-1) showing a lunar activity rhythm. Shaded areas show moonlight hours. Circle shows full moon. Explanation see text

Seven platypuses were equipped twice with data-loggers during this study, with a break between deployments of six to 21 months. It is interesting to note that six out of these seven individuals showed the same activity pattern in both experiments. Only one female changed her activity pattern from diurnal (in winter) to nocturnal (in summer) (06-99-3 & 12-99-1, see App. A). Five of the seven animals equipped twice were caught at the same site in both cases.

In summary, platypus behaviour while foraging varied considerably between individuals. Activity patterns were dependent on a number of factors including sex, season, light levels as well as water and air temperatures. Season and (auto correlated) water temperature played a vital role in platypus behaviour. At colder temperatures (i.e. in winter), dive, surface and foraging durations were longer and activity levels were higher. On a daily scale, platypuses changed their behaviour clearly in response to light levels, which affected dive and surface durations as well as dive depths. Results are summarised in Tab. 6-5.

<i>Variable:</i>	<i>dive</i>	<i>surface</i>	<i>dive</i>	<i>foraging</i>	<i>activity</i>	<i>no. of dives</i>
<i>dependant on:</i>	<i>duration</i>	<i>duration</i>	<i>depth</i>	<i>duration</i>		<i>per hour</i>
sex	+	+	+	-	-	+
season	+	+	+	+	+	+
dive duration		+ (↑)				
dive depth	+ (↑)	-				
water temperature	+ (↓)	-		-	+ (↓)	+ (↑)
air temperature	+ (↓)	-		-	-	-
light levels	+ (↓)	+ (↓)	+ (↓)			+

Tab. 6-5: Effects of different factors on behavioural variables of platypuses at Lake Lea (+ significant effect (positive (↑) / negative (↓) correlation), - not significant, +/- significant only in part of the data)

6.3.3 Behavioural observations and population dynamics

Visual observations of the foraging behaviour of both platypuses equipped with transmitters and other platypuses in the study area were made during the trapping sessions. Foraging behaviour of platypuses consisted of swimming or floating on the water surface, diving nearly vertically to the bottom, then swimming along the substrate and returning to the surface to process food before the next dive. During descent, platypuses propelled them-

selves under the water by rapid and alternate beats of their forelegs. Between the dives, platypuses were usually floating quietly or swimming slowly along the surface. In most cases, only the bill and the top of the head was visible, though sometimes also the whole back and part of the tail were exposed.

Net avoidance behaviour was observed in a number of animals caught previously. Platypuses tried to avoid the nets by diving underneath them, by climbing over them or simply by walking around them. In some cases, the animals returned to their burrows after thoroughly exploring the nets. However, in most cases they showed a very high degree of inquisitiveness. Eventually, they were either able to work their way through the nets or were caught.

To gain insight into the population dynamics of platypuses at Lake Lea, social units were identified by analysing data from trapping sites 1, 2, 3, 6, 7 and 9 (see Fig. 2-3) in regards to gender as well as status of the animals (transient or resident) (data from experimental animals and other animals caught during concurrent studies were analysed, see Chapter 2.2.2). The results (summarised in Tab. 6-6) show a high tolerance of animals to share burrow areas. Up to six resident females were found to share the same trapping site (event 3, Tab. 6-6). On 12 occasions, more than one resident male (up to three) was captured at the same burrow area.

During field trips conducted in winter 1998 for example (event 6, Tab. 6-6) two resident males, two resident females and one transient male were trapped at site 3. The animals showed temporal separation with one resident male being active at night while the other resident and the transient male showed 'mixed' activity. In June 1999 (event 8, Tab. 6-6), the same resident male (06-99-4) was caught in burrow area 3 with two other resident males and one transient male as well as with three resident females. Again, the resident male was nocturnal while one of the other resident males showed 'mixed' activity (third resident males' activity pattern unknown). This suggests a dominance of the resident nocturnal male. Two of the three observed females were diurnal while the third one showed nocturnal activity.

<i>Event</i>	<i>Trapping Site</i> (i.e. burrow area)	<i>Date</i>	<i>resident male</i> total no., thereof with logger identity (rhythm)	<i>resident female</i> total no., thereof with logger identity (rhythm)	<i>transient male</i> total no., thereof with logger identity (rhythm)	<i>transient female</i> total no. (none with logger)
1	1. Bonds/Calf Creek	Nov 98	1 -	1 10-98-4 (mixed)	5 10-98-3(nocturnal)	1
2	2. Jennifer Creek	Jul 99	2 07-99-1 (nocturnal) 07-99-2 (nocturnal)	0 -	1 -	0
3	3. Deep Hole	Jan 98	3 -	6 -	1 -	2
4	3. Deep Hole	Feb 98	1 -	3 -	0 -	0
5	3. Deep Hole	Mar 98	3 -	4 -	1 -	0
6	3. Deep Hole	May/Jun/Jul 98	2 05-98-2 (mixed) 06-99-4 (nocturnal)	3 04-98-3 (noc, subad.) 04-98-4 (nocturnal)	2 07-98-1 (mixed)	0
7	3. Deep Hole	Jan 99	1 -	1 -	1 01-99-3 (mixed)	0
8	3. Deep Hole	Jun 99	3 06-99-4 (nocturnal) 06-99-2 (mixed)	3 06-99-6 (nocturnal) 06-99-1 (diurnal) 06-99-3 (diurnal)	1 -	0
9	3. Deep Hole	Dec 99/Jan 00	3 12-99-2 (mixed) 12-99-3 (mixed) 01-00-4 (nocturnal)	3 01-00-1 (nocturnal)	0 -	0
10	3. Deep Hole	Feb 00	3 01-00-4 (nocturnal)	3 01-00-1 (nocturnal)	0 -	0

Tab. 6-6/1: Social units identified in the platypus population at Lake Lea (trapping sites see Fig. 2-3, data-logger-files (actograms) see Appendix A, explanations see text).

<i>Event</i>	<i>Trapping Site</i> (i.e. burrow area)	<i>Date</i>	<i>resident male</i> total no., thereof with logger file (rhythm)	<i>resident female</i> total no., thereof with logger file (rhythm)	<i>transient male</i> total no., thereof with logger file (rhythm)	<i>transient female</i> total no. (none with logger)
11	6. Bare Mount Creek	Feb 98	1 -	3 02-98-4 (nocturnal)	0 -	0
12	6. Bare Mount Creek	Mar 98	1 -	2 02-98-4 (nocturnal) 03-98-5 (mixed)	1 03-98-4 (mixed)	0
13	6. Bare Mount Creek	Jul/Aug 98	2 -	2 07-98-4 (nocturnal) 02-98-4 (nocturnal)	2 -	0
14	6. Bare M. Creek	Nov 98	1 10-98-2 (mixed)	2 12-98-1 (mixed)	0 -	0
15	6. Bare M. Creek	Dec 99/Jan 00	1 12-99-4 (nocturnal)	1 12-99-1 (nocturnal)	2 -	0
16	7. Platypus Play- ground	Feb 99	2 01-99-4 (mixed) 02-99-2 (nocturnal)	1 02-99-1 (mixed)	0 -	0
17	7. Platypus Play- ground	Jan 00	3 12-99-4 (nocturnal) 01-00-3 (nocturnal)	0 -	0 -	0
18	9. Lea River	Feb 98	2 -	2 -	0 -	2
19	9. Lea River	Apr/May 98	3 04-98-4 (nocturnal, subadult)	4 03-98-5 (mixed) 05-98-3 (nocturnal)	2 -	0
20	9. Lea River	Jan 99	1 -	2 12-98-1 (mixed)	0 -	0

Tab. 6-6/2: Social units identified in the platypus population at Lake Lea (trapping sites see Fig. 2-3, data-logger-files (actograms) see Appendix A, explanation see text)

A comparable pattern was also observed for example in summer 1999/2000 (event 9, Tab. 6-6). Three resident males and three resident females were caught at site 3. While one of the three resident males was nocturnal (01-00-4), the other two males showed 'mixed' activity patterns. After one month, (event 10, Feb 2000) the resident nocturnal male (01-00-4) was still using trapping site 3, however, this time together with two resident males other than those from event 9. This again suggests a dominance of the resident nocturnal male.

6.4 Discussion

6.4.1 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 in the swim tank (see Chapter 4.3.2). 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 in 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 and the energy expenditure of platypuses in their natural habitat cannot be ruled out. Platypuses at Lake Lea are considerably larger than animals from most other populations (see Chapter 2.2.4) which makes it easier to equip them with data-loggers due to their greater payload capacity. Increased care and the use of even smaller devices is indicated if experiments with data-loggers are to be attempted on smaller individuals.

Both types of data-loggers used were suitable for measuring platypus behaviour. However, the TDRs were clearly more useful in terms of endurance and versatility. The measurement of dive duration at two-second intervals allows a detailed analysis of diving behaviour. The memory of the TDRs was big enough to record up to 11 days of detailed foraging behaviour. In addition, the TDRs were much better protected against abrasion and environmental im-

pacts. The burrowing lifestyle of the platypuses puts data-loggers of any kind under very high mechanical stress, probably much higher than when used with penguins for example. The casing must withstand water but also earth, mud, root impact and platypus grooming. The TDRs showed some problems in this respect, especially in the area of the sensors at the back of the devices, and failed in a number of cases.

Activity loggers had even bigger endurance problems. After numerous failures, they were protected against leakage and abrasion with an additional casing of marine epoxy, which increased weight and size of the devices. However, if the aim of a study is the long-term observation of activity levels in platypuses, the activity loggers are the more useful devices. In addition, time-depth recorders are only useful in habitats where a water depth of at least 50 centimetres is expected. Although very sensitive, pressure sensors would otherwise not be able to record dive profiles accurately.

6.4.2 Dive and surface durations

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. It is interesting to note that dive durations of captive animals are generally reported to be shorter than dive durations of platypuses in the wild (Scheich et al. 1986, Evans et al. 1994). The observations in the swim tank confirm these findings. Reported dive and surface durations of platypuses are summarised in Tab. 6-7.

<i>Mean dive duration</i>	<i>Max. dive duration (wedging)</i>	<i>Surface duration</i>	<i>No. of dives</i>	<i>Site/Comment</i>	<i>Reference</i>
30-60 s					Allport (1878)
120-180 s	10 min				Burrell (1927)
14 s	1 min			holding facility	Scheich et al. (1986)
	>6 min			holding facility	Jones et al. (1987)
34.8 ± 11.9 s		12.7 ± 6.9 s	437	Armidale, NSW	Kruuk (1993)
14-34 s	3.4 min	16-18 s	670	Duckmaloi Weir, NSW	McLeod (1993)
45-50 s				Broken River, QL	Lamm (1993)
28 ± 1 s	11 min	73 ± 5 s	488	holding facility	Evans et al. (1994)
30-60 s					Grant (1995)
20-40 s		10-20 s		Goulbourn River, VIC	Gust & Handasyde (1995)
51.9 / 54.4 s		12.9 / 8.5 s	337/97	Bathurst, NSW	Benson (1997)
28.3-33.3 s		11.8-20.3	303	Lake Lea, TAS	Otley et al. (2000)
23.5 ± 9.9 s	5 min		555	holding facility	this study
31.3 ± 4.0 s	2.3 min	10.1 ± 2.0 s	90647	Lake Lea, TAS	this study

Tab. 6-7: Comparison of dive durations and surface durations recorded for platypuses

6.4.3 The organisation of the dive cycle and dive depth

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. Indeed, diving of platypuses at Lake Lea was influenced by a number of factors including season, sex and light levels. In addition, both dive and surface duration were dependent on dive depth. Also, a correlation between surface duration and corresponding dive duration was observed (see Tab. 6-5). These observations confirm results obtained by Kruuk (1993) who reported that dive times increased significantly with water depth. Consistent with the observations of Kruuk (1993), a low but significant positive correlation between dive and surface duration was found in this study.

However, results presented here suggest that the most important variable explaining differences in dive and surface durations of platypuses is water

level. Changes in dive depth over the year due to changing water levels are most likely responsible for the observed dependency of dive and surface duration on season. Otley et al. (2000) noted that water depth is related to many parameters that determine habitat quality for platypuses, e.g. light, temperature, oxygen levels and substrate sediment size all of which influence the macro-invertebrate abundance and distribution (Williams and Feltmate 1992). Otley et al. (2000) reported that individuals at Lake Lea appeared to prefer foraging close to the lake shore rather than in the lake centre. Consistent with these results, a preference for foraging in shallow depths was found in this study. Ninety-eight percent of all dives recorded went to depths of less than 3 metres and 48 % to less than one metre (Fig. 6-5). This result is consistent with recorded foraging depths of up to three metres in river systems (Bryant 1993, McLeod 1993). A preference for foraging in shallow water appears to be shared by other small semiaquatic species including otters (Melquist and Hornocker 1983, Nolet et al. 1993, Kruuk 1995) and mink (Birks and Linn 1982).

In this respect, it comes as a surprise that platypuses did not appear to move to shallower depths in winter when water levels at Lake Lea were up to 60 cm higher than in summer. Instead, as indicated through dive depths, the animals appeared to keep the same foraging locations throughout the year. 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.

Maintaining the same foraging locations throughout the year, however, causes energetic disadvantages through deeper diving in winter. How do platypuses make up for these disadvantages? 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 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.

For the first time, the techniques used in this study enabled the measurement of bottom duration (amount of time spent searching for prey) of platypuses in the wild. Although longer descent and ascent times already prolonged dive durations in winter, bottom duration was higher in winter than in summer (Fig. 6-18). Interestingly, the ratio between bottom and dive duration remained constant throughout the year (Tab. 6-8).

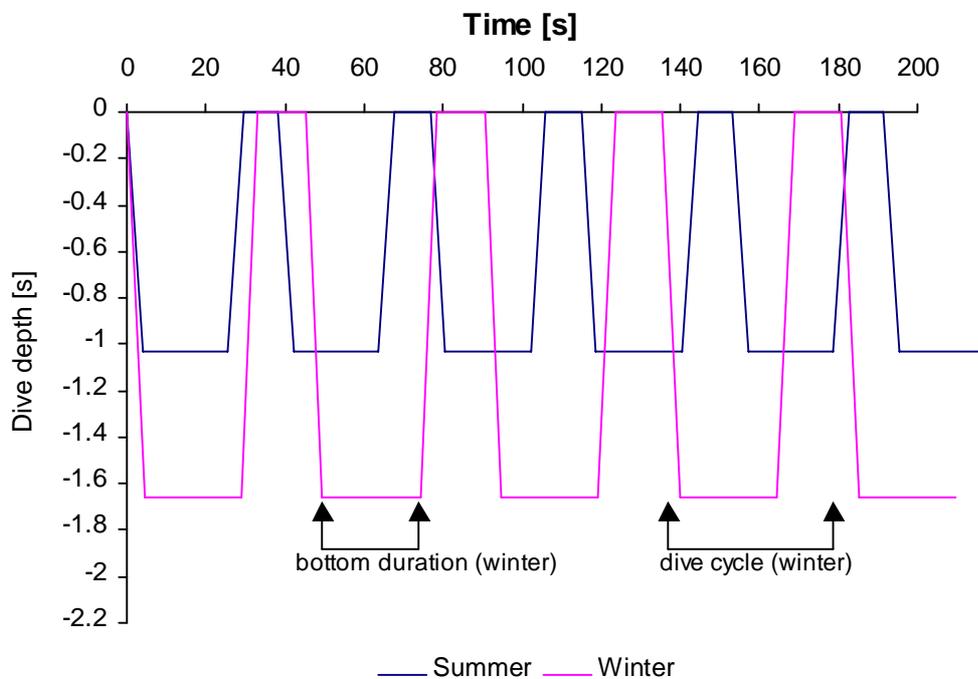


Fig. 6-18: Typical diving pattern of platypuses at Lake Lea in summer (blue) and winter (red), based on average values for dive, bottom and surface duration as well as dive depth

In both summer and winter, 74 % of the whole dive duration was spent on the bottom of the habitat 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 sea-

son (Tab. 6-8). 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 observed ratios between bottom and dive respectively dive cycle duration are likely to present the optimum in order to balance energetic costs with energy intake during the platypus's oxygen limited hunt.

	<i>Summer</i>	<i>Winter</i>
Dive duration [s]	29.2	34.4
Bottom duration [s]	21.7	25.3
Surface interval [s]	9.2	11.9
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

Tab. 6-8: Diving behaviour parameters of platypuses at Lake Lea in summer and winter. Ratios between bottom and dive duration as well as searching efficiency remain nearly constant regardless of season (see text)

Kramer (1988) put forward a model of optimal recovery time, the so-called optimal breathing theory. It is based on the assumption that the diver maximises its long-term rate of energetic gain during foraging by optimising surface durations. 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 (see also Nolet et al. 1993, Houston and McNamara 1994). The hypothesis 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 in-

crease with depth (Wilson and Wilson 1988). In the platypus, the energy gained from a dive is clearly proportional to bottom duration and the results of this study indicate that indeed bottom duration as well as dive and surface duration increase with increasing dive depth. Therefore, platypuses clearly seem to follow the optimal breathing theory proposed by Kramer (1988).

6.4.4 Seasonal differences in diving behaviour

Although searching efficiency (prey search time per unit foraging time) remains nearly constant throughout the year, foraging efficiency (i.e. foraging gain per unit effort) is likely to decrease in winter. This and other studies (e.g. Grant and Dawson 1978a) suggest that lower water temperatures increase the platypus's energy consumption profoundly. Colder temperatures in winter are likely to contribute to changes in diving behaviour as they result in higher thermal stress. Indeed, dive and surface durations increased with decreasing air and water temperature, respectively. At the same time, prey abundance is likely to decrease during winter. Faragher et al. (1979) and Lamm (1993) reported reduced item size and diversity of benthic organisms over winter months. Also, Otley (1996), who radio-tracked male and female platypuses in summer and winter at Lake Lea, suggested lower prey densities in winter.

How do platypuses cope with the reduction in prey availability in the winter months in combination with higher energetic costs due to lower temperatures? As discussed above, the optimisation of bottom time, i.e. the time available for prey searching, is an essential factor for foraging efficiency in the platypus. One possibility to increase overall bottom time is the extension of the daily foraging duration. Foraging durations of platypuses at Lake Lea were on average one hour longer in winter than in summer. Despite the fact that platypuses have to dive deeper during the cold season at Lake Lea, calculation of total bottom duration per day (by multiplying foraging duration with bottom / dive cycle duration ratio, see Tab. 6-8) yields a higher value for the winter months (6.70 h day^{-1}) than 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 suggested by Faragher et al. (1979) or the shift to an energetically less demanding diurnal activity pattern, a behaviour that will be discussed in detail below.

Another strategy that the platypus may utilise to increase foraging efficiency in winter would be to increase total bottom duration by shortening the surface intervals between dives. Kruuk (1993) suggested that time on the surface is predominantly related to the processing of prey, and time on surface may therefore be related to the quantity or type of food caught during the dive. Surface durations, however, were longer in winter than in summer in this study and there is no obvious reason to believe neither that food processing should take longer in winter nor that the quantity of food increases in the cold season.

Therefore, surface intervals of platypuses must be dependent on additional variables other than the time for food processing. Although the platypus was found to dive mainly aerobically (see below, Chapter 6.4.8), replenishment of body oxygen stores and a limited oxygen capacity are the most likely reason for the prolonged surface intervals in winter. Accordingly, a low but significant relationship between dive duration and subsequent surface duration and a lower dive/surface duration ratio was observed in winter (Tab. 6-8). This suggests that in winter body oxygen stores are exceeded more frequently than in summer with the need for prolonged surface intervals to eliminate waste products formed during anaerobic metabolism. The relatively low aerobic dive limit that was estimated in this study supports this view (see Chapter 6.4.8).

6.4.5 Foraging efficiency and dive/surface duration ratios

The observations of this study on platypus dive cycles during different seasons also challenge the theory of Kruuk (1993) who suggested that the ratio between dive and surface durations could be used as a measure of foraging efficiency in the species. Kruuk (1993) studied platypuses in water bodies with different eutrophic levels and found that dive/surface duration ratios became significant larger with lower insect densities. In the eutrophic areas dive/surface duration ratio was as low as 1.5, in the oligotrophic ones as high

as 3.9. Kruuk (1993) suggested that the less time platypuses spend under water the more successful their hunt. Also, the less time spent on the surface the less prey was caught and therefore less processing time was required. Consequently, a lower dive/surface duration ratio would mean a greater foraging efficiency in the species (Kruuk 1993).

Results obtained in this study, however, indicate that this theory might be too simplistic. A lower dive/surface duration ratio (i.e. following Kruuk 1993 higher foraging efficiency) was found in winter (Tab. 6-8). Following Kruuk (1993) this would imply higher prey densities in the cold season, which is highly unlikely (see above and Faragher et al. 1979, Lamm 1993, Otley 2000). Kruuk (1993) argued that in a diving multi-prey loader like the platypus (in contrast to single prey loaders like otters) time on the surface must be used to process captured prey during almost every surface interval. However, the extent of this food processing during active foraging is questionable and in view of the results of this study unlikely to be a major factor determining surface duration. 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 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 one minute duration occurred on average after each 25th dive, which seems to be a reasonable number to collect a decent “mouthful” of prey. The low foraging efficiency in winter found in this study (mean: 2.89) is 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.

This is not the first study to question the assumptions of Kruuk (1993) in calculating foraging efficiency. Benson (1997) noted that the theory of Kruuk (1993) implied that all recordings of dive and surface times are associated with the platypus’s foraging activity and not with other aspects of platypus

behaviour such as travelling between patches or courtship and mating activity. In addition, Otley (1996) suggested that the assumption of Kruuk (1993) of equal foraging ability between individuals was not completely applicable. Despite reasonably homogenous habitats, both Otley (1996) and McLeod (1993) found highly variable dive/surface duration ratios between animals in their studies. Also, Benson (1997) found dive/surface ratios very variable and this study confirms these findings.

To conclude, 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 (this study, Krueger et al. 1992, Hawkins and Fanning 1992, Grant 1983a). 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 can be assessed by measurement of platypus bottom durations with longer total bottom duration suggesting a less productive environment. Extended total bottom durations and foraging durations in winter found in this study confirm this suggestion.

6.4.6 Gender differences in diving behaviour

This study also found differences in dive duration, dive depth and surface interval between male and female platypuses, respectively, with male platypuses diving longer and deeper (+40 cm) than female platypuses. Male and female platypuses seemingly chose different foraging locations in Lake Lea with males preferring slightly deeper waters. Shallower depths are easier to reach and generally provide a more suitable habitat for platypuses, mainly because light levels and thus vegetation and invertebrate densities are higher (e.g. Otley

et al. 2000). Then what is the advantage of foraging at greater depths to the male platypus? Obviously, male platypuses are more suited for deeper and energetically higher demanding foraging activity because of their size. A bigger body means less heat loss and swim tank experiments show that male platypuses use relatively less energy than female platypuses during foraging. In addition, the ratio between bottom duration and dive duration was higher in male platypuses compared to females. This suggests that, despite deeper diving, males are capable of using a higher percentage of their dive duration for prey search.

Secondly, prey preference might help to explain the observed gender differences. Preliminary results indicate that there are differences in diet selection between males and females and season and that a higher variety of preys are taken in the winter months (Munks et al. 2000). Male platypuses at Lake Lea might prefer different prey species than females, such as prey species that are more abundant in deeper waters. However, at this stage, this is only speculation and further research is needed.

6.4.7 Maximum dive times

Platypuses are known to spend extended periods of time 'wedging' (Scheich et al. 1986), i.e. inactive resting under the water surface. However, reports on maximum dive times differ in the literature (Tab. 6-7) and most observations were made in holding facilities rather than in the wild. Jones et al. (1987) reported 'wedging' in excess of six minutes in captive platypuses while Evans et al. (1994) recorded resting periods under the water surface of up to 11 minutes duration. Other authors report maximum dive times of 10 minutes (Burrell 1927), one minute (Scheich et al. 1986), 2.33 min (McLeod 1993) and 5 min (this study, in swim tank).

In Chapter 4.4.2, the physiological adaptations of platypuses for this behaviour were discussed. In combination with the low metabolic rate during 'wedging' reported in this study, these adaptations suggest that platypuses are indeed able to stay inactive under water for extended periods of time. However,

the results of this study also suggest that inactive diving in platypuses is much more limited than previously thought. Fourteen animals were observed at Lake Lea over several days each during more than 1100 hours of foraging. Out of more than 88000 dives performed during this time, only 10 dives were longer than 80 s with a maximum dive duration of 138 s. This indicates that 'wedging' is not a common but merely an emergency behaviour, which is rarely used in the wild. Consistent with this observation, calculation of the aerobic dive limit (see Chapter 6.4.8) for the inactive platypus derived from the 'wedging' rate (3.56 W kg^{-1}) yields 140 seconds. Maximum dive times in the wild close to this value are likely for the platypus because longer dive times would require anaerobic metabolism and thus potentially dangerous post-dive recovery periods on the water surface.

This suggestion is consistent with results obtained by Johansen et al. (1966), who questioned the long dive times estimated by earlier authors and reported dive times of around three minutes to be close to the endurance limit of the animal. McLeod (1993) reported maximum dive times of 140 seconds 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 during this study in holding facilities are likely to be typical for animals in captivity where possibilities for hiding are limited. This study suggests that in emergency situations in the wild 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 due to oxygen depletion. 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. The same behaviour was observed on some occasions during 'wedging' periods in the swim tank (Chapter 4.3.1).

6.4.8 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). If the ADL is exceeded, anaerobic metabolism begins to take over and metabolic end products, such as lactic acid, accumulate. In consequence, 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 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 versus dive duration could yield an estimation for the ADL. However, simple inspection of post-dive surface intervals is problematic since platypuses may revive despite carrying an increased lactate load. To minimise this error, dive and surface durations were averaged over three consecutive dives, which was the minimum number to obtain a relationship between minimal surface duration and dive duration (see for comparison Horning 1992, Pütz 1994, Bethge et al. 1997). Regression of mean dive duration against mean surface duration yields minimal surface times for aerobic diving (Fig. 6-19, solid line). ADL was estimated to be 40 s. The minimal surface duration for dives lasting longer than the estimated ADL is best described by surface duration [s] = 0.37 dive duration [s] – 14.9 (Fig. 6-19).

ADL can also be calculated from the product of the oxygen stores before a dive and the energy equivalent for oxygen divided by the power requirements for foraging. The oxygen carrying capacity of platypus blood is 23 ml O₂ per 100 ml blood (Grant 1995). However, total blood volume of the platypus is not

known, but haematocrit, haemoglobin concentration and oxygen-carrying capacity have been shown to be high (Evans et al. 1994). Evans et al. (1994) estimated myoglobin oxygen stores in platypuses of about 5 ml per kg body mass and a total oxygen store of a one-kg platypus at the beginning of a dive to be 25 ml. A calculation of ADL from the product of this oxygen stores prior to a dive and the energy equivalent for oxygen (20.11 kJ/l O₂) divided by the power requirements for foraging $P_{\text{(FORAGE)}}$ (see Chapter 4.3.2) produces a value of 59 seconds.

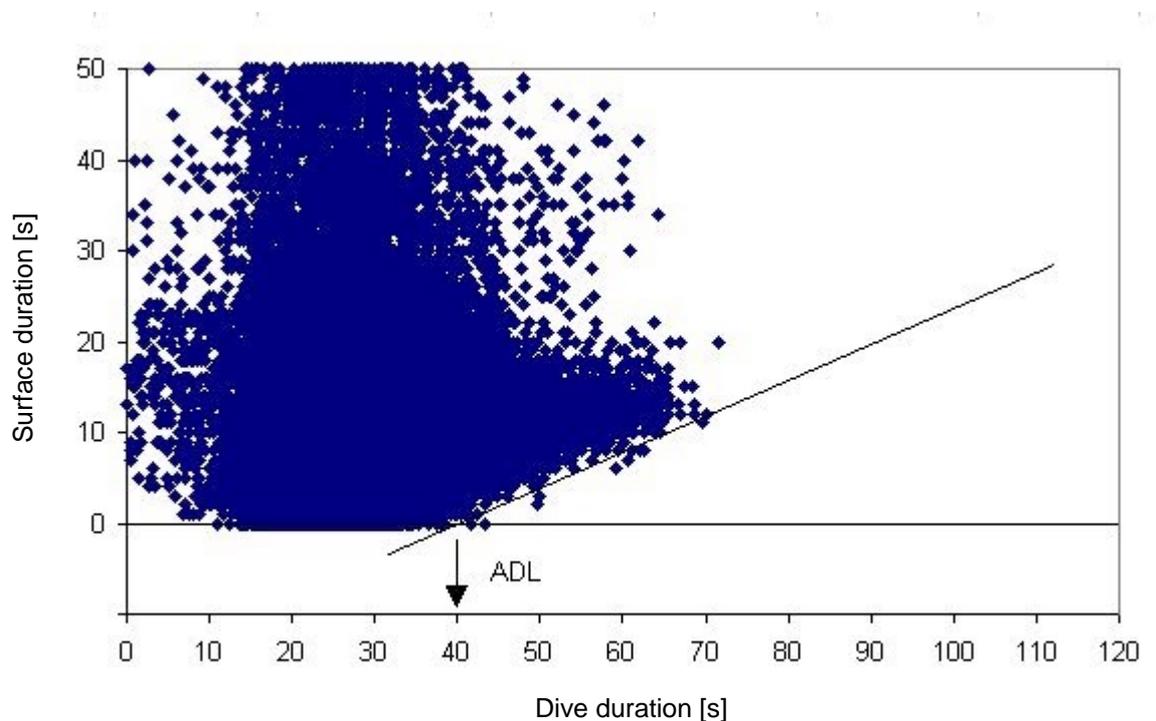


Fig. 6-19: Mean dive duration plotted against mean post-dive surface duration of platypuses at Lake Lea (n=88906). Solid line describes minimal surface duration. Arrow shows proposed ADL (40 s)

This ADL is consistent with the results of Evans et al. (1994) who suggested that during active diving oxygen stores of the platypus would be depleted after 60 seconds. However, the ADL derived from dive and surface durations measured in the wild is substantially lower and the difference can be attributed to a number of causes. It was suggested before that energetic costs

for diving derived in the swim tank are likely to underestimate energetic needs in the wild (see Chapter 4.4.1). Indeed, the distribution of dive durations in the wild (Fig. 6-3, Fig. 6-20) suggests that an ADL of 40 s is more likely for the platypus than the higher value. Seventy-two percent of all dives in the wild ranged between 18 and 40 s (Fig. 6-20). 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). On the other hand, depleting oxygen stores and consequently using anaerobic metabolism results in longer times at the surface between dives. Reduced foraging success is the consequence. Accordingly, only 15 % of all dives derived from time-depth recorders in the wild exceeded the estimated ADL of 40 s (Fig. 6-20). At the same time, the swim tank experiment indicates that short dives are inefficient for the platypus (see Fig. 4-3). Accordingly, only 13 % of all dives were shorter than 16 seconds (Fig. 6-20).

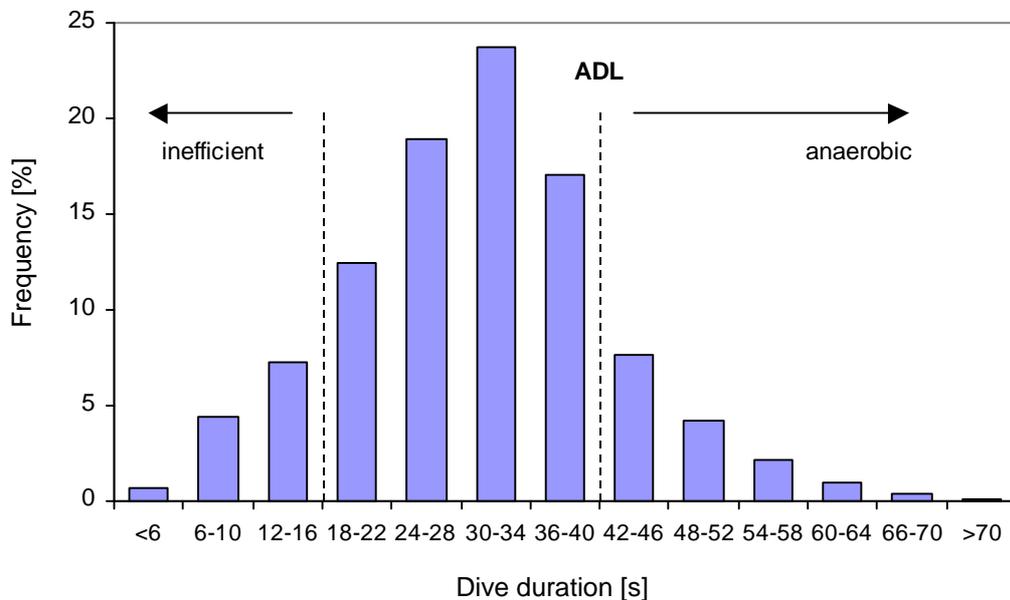


Fig. 6-20: Frequency diagram of platypus dive durations at Lake Lea (n=90647). Proposed ADL shown (40 s)

A calculation of average power requirements of platypuses in the wild from the product of the oxygen stores prior to a dive (25 ml, Evans et al. 1994) and the energy equivalent for oxygen (20.11 kJ/l O₂) divided by this ADL produces a value of 12.57 W kg⁻¹. Consequently, it can be estimated that energetic costs derived in the swim tank (8.48 W kg⁻¹) underestimate power requirements in the wild by up to 48 %.

The low percentage of dives exceeding the ADL suggests that there is little need for anaerobic metabolism during normal diving behaviour in the platypus. This view is supported by the characteristics of platypus skeletal muscle. Evans et al. (1994) and Jones et al. (1987) found that the distribution and properties of LDH isoenzymes in skeletal muscle of the platypus do not suggest heavy dependence on anaerobic glycolysis. The ability of platypus muscles to buffer metabolic acids that accumulate during anaerobiosis was low relative to other diving mammals (Evans et al. 1994). From their estimate of available oxygen stores and oxygen consumption rate, Evans et al. (1994) suggested that there is little need for anaerobic metabolism during normal dives. Also, Johansen et al. (1966) studied forced diving in two platypuses and found no significant drop in blood pH after surfacing, despite an apparently well-developed vasoconstriction during the dive. Johansen et al. (1966) suggested that accumulation of lactic acid during the forced dives was modest or that it was entirely masked by reserve buffer mechanisms. However, they noted that the buffering capacity of blood was poor indicating little anaerobic metabolism.

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 seconds (this study), then returning to the surface for a mean recovery period of 10.1 seconds (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 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 (see Chapter 6.4.7).

6.4.9 Active period and foraging duration

Some early researchers questioned the ability of the platypus to forage in water for very long time. Burrell (1927) for example reported that platypuses venture out in the early morning and evening only, spending not more than two hours in water in any one day. Also, Smyth (1973) postulated that in the field platypuses are poor thermoregulators and probably spend only brief periods in the water in winter, returning frequently to the bank or burrow to warm up. However, it is now widely accepted that platypuses can spend extended periods in the water and that the thermoregulatory mechanisms of the animal are excellent (Grant and Dawson 1978a, Grant and Dawson 1978b).

Reports on the duration of active periods in platypuses differ and range from 7 to 19 hours (Tab. 6-9). Grant et al. (1992) investigated platypuses in the lower Thredbo River, NSW, from several days up to five months and found that individuals rested in burrows for between 5.25 and 15.1 (mean 10.7) hours at a time. Gust and Handasyde (1995) recorded mean active periods of about 10 hours per day. Serena (1994) reported an individual mean duration of burrow occupancy between 11.6 and 16.7 hours per 24-hour period. Also, Grant (1983b) found that platypuses spent 40 to 51 % of their time in water. Otley et al. (2000) reported that platypuses at Lake Lea foraged for between 8.5 and 16 hours per 24-hour period (Tab. 6-9).

Mean individual active periods (10.0 to 15.75 h) found in this study are in line with findings of Grant et al. (1992) (Thredbo River, NSW) and Otley et al. (2000) (Lake Lea) but are slightly higher than records from Badger Creek (Serena 1994) and Goulbourn River (Gust & Handasyde 1995) in Victoria as well as Shoalhaven River, NSW (Grant 1983). This observation is consistent with Serena (1994), who stated that the mean time spent in dens by Thredbo

platypuses (Grant et al. 1992) was less than for any of the platypuses monitored along Badger Creek.

<i>Mean active period [h]</i>	<i>Habitat</i>	<i>Source</i>
9.6 - 12.2	Shoalhaven River, NSW	Grant (1983)
8.9 - 18.8 *	Thredbo River, NSW	Grant et al. (1992)
7.3 - 12.4 *	Badger Creek, VIC	Serena (1994)
9.8 - 10.5	Goulbourn River, VIC	Gust & Handasyde (1995)
8.5 - 16	Lake Lea, TAS	Otley et al. (2000)
10.0 - 15.8	Lake Lea, TAS	this study

Tab. 6-9: Comparison of active periods recorded for platypuses (*derived from burrow times)

The differences in foraging duration between habitats could well be related to different climatic conditions. Both Lake Lea and the Thredbo River in Australia's Southern Alps are very cold habitats where water temperatures frequently approach 0°C in the winter months. Platypuses at Lake Lea foraged on average one hour longer in winter than in summer. Activity levels were significantly higher during the winter months than during summer (Fig. 6-8). Consistent with this, Lamm (1993) found that water temperature affected the active time of a female platypus on her study site with activity decreasing with higher water temperatures. Also, Otley et al. (2000) observed longer foraging bouts during winter than during summer.

Longer foraging durations in winter are plausible not only because of increased energetic demands but also because item size and diversity of benthic organisms over the winter months are most likely reduced (Faragher et al. 1979, Lamm 1993). Other factors which may contribute to seasonal variation in the length of time that platypuses forage include the degree of food competition with other platypuses or other species including fish or water rat, or for example incidence of flooding and high water levels (Temple-Smith 1973, Grant and Carrick 1978, Faragher et al. 1979, Grant and Temple-Smith 1983, Benson 1997, Otley et al. 2000).

Methods used in this study allowed the constant observation of platypus behaviour in detail over a number of consecutive days. Data-logger recordings show a surprisingly high variability in the duration of the active period (3.40 to 30.83 hours) with continuous foraging (i.e. time with diving activity as measured by time-depth recorders) of up to 29.83 hours. Consistent with earlier reports (Grant 1995, Otley et al. 2000), animals foraged continuously with only short breaks (most of them less than three minutes duration) between feeding bouts.

The use of activity loggers also allowed elucidation of the temporal organisation of the active period. Consistent with results for a number of other species (Refinetti 2000), platypuses at Lake Lea showed the highest activity levels at the beginning and towards the end of their foraging trip while the level of activity did not change significantly during the rest of the active period (Fig. 6-10). Consequently, in nocturnal and diurnal animals (65 % of all observed animals), highest activity levels occurred during twilight, a time where activity levels of many animals are found to be increased (Cloudsley-Thompson 1980). For small carnivores, twilight is generally regarded as the best time to hunt. The relatively dim light provides partial protective cover from predators. At the same time, visibility is still better than at night (Cloudsley-Thompson 1980). In platypuses, increased activity during twilight (crepuscular activity) is well established (e.g. Grant 1983a, Grigg et al. 1992) and might relate to increased prey availability. Many macro-invertebrate insect families show active periods just after sunset and before dawn in river systems (Williams and Feltmate 1992) and this might also be true for lake systems.

Light levels also had an influence on dive cycles of platypuses at Lake Lea. Dive profiles of some animals revealed that they clearly explored greater depths during daylight hours than during the night (12-98-1, 12-99-2 and 01-00-1, see Appendix A), a behaviour that most probably relates to a change in foraging location between day and night time. In general however, light conditions resulted in shorter dive cycles with both dive duration as well as surface duration being reduced. Also, the number of foraging breaks, i.e. resting

periods of more than one minute duration, was less during the day compared to nighttime (Fig. 6-7). This behaviour is likely to be a strategy to avoid predators more effectively during light conditions as time spent at any one place on the lake surface is reduced.

Finally, it is interesting to note that platypuses seem to start and end their day with some minor activity in their burrows. Activity loggers showed that the beginning of each active period was characterised by low activity levels lasting for an average of 50 minutes. Correspondingly, at the end of each active period, low activity levels for an average of 21 minutes were observed. Activity levels appear too low for burrowing or some other energetic behaviour, which suggests behaviours like grooming or waking up during these periods.

6.4.10 Inactivity

The question of inactive periods, torpor or hibernation is still not conclusively answered for the platypus. Several species of small mammals enter daily torpor or hibernation, especially if food-deprived (Geiser and Ruf 1995, Refinetti 2000), and there is some evidence of torpor or prolonged inactivity in platypuses in captivity as well as in the wild (Eadie 1935, Fleay 1944, Serena 1994). Fleay (1980) for example reported the case of an adult female housed outdoors at Healesville Sanctuary, Victoria, that remained inactive for 14 periods, ranging in length from 24 to 156 hours. Serena (1994) reported prolonged inactivity of two grown females during winter in the wild of up to 154 hours. Grant (1983a) noted that, unless the animal was capable of becoming torpid, the added thermal stress in winter would force the platypus to spend at least the same amount of time feeding in winter as in other seasons.

This and other studies (Grigg et al. 1992, Grant et al. 1992, Otley et al. 2000) have confirmed that platypuses are capable of foraging for long periods of time under icy conditions. Although activity patterns at Lake Lea were observed over two consecutive winters, the longest period of inactivity observed during this study was 27.20 h, which happened to be in summer (02-99-1, see App. A). Also, Otley et al. (2000) found that individuals at Lake Lea fed con-

tinuously during their active period, even during the winter months. Grigg et al. (1992) monitored body temperature of free-ranging platypuses throughout winter in the Thredbo River and found platypuses active every day. No evidence of hibernation or even brief periods of torpor was observed. All individuals maintained body temperatures close to 32°C throughout the winter. Grigg et al. (1992) concluded that bouts of torpor or hibernation are most unlikely to be a routine occurrence in healthy platypuses, and the results of this study confirm these findings. The platypus is clearly not a spontaneous hibernator like its relative, the echidna, which shows regular annual pattern of hibernation (Nicol and Anderson 2000, Grigg and Beard 2000). Platypuses might still be facultative hibernators, which enter hibernation in response to food scarcity (Nicol, personal communication). Yet, no evidence for such behaviour was found in this study.

Female platypuses are believed to spend several days to weeks in their burrow without or with only short periods of foraging while raising their young during the breeding season (Grant 1983a, Grant 1995). However, so far only anecdotal evidence exists for this behaviour and no studies have confirmed or clarified this breeding habit. The activity loggers would allow a detailed study of the activity patterns of platypuses during breeding. Unfortunately, during this study, no lactating females were caught, which could have been equipped with data-loggers, although two breeding seasons of platypuses at Lake Lea were covered.

6.4.11 Rhythm and activity pattern

The results of this study suggest that activity pattern of platypuses are much more variable than previously reported. Individual animals showed considerable variation in their daily emergence and return times. A high percentage of animals had irregular activity patterns. This suggests that activity rhythms of platypuses do not solely rely on the light dark cycle but also depend quite considerably on a number of other ecological and physiological factors. Previous studies have already noted that for example social organization, ma-

ting system, competition between individuals, abundance and dispersion of food, predator avoidance or thermoregulation costs are likely to influence platypus activity pattern in the wild (Grant et al. 1992, Serena 1994, Gardner and Serena 1995, Gust and Handasyde 1995, Francis 1999, Otley et al. 2000).

Most studies on the behaviour of platypuses have been on populations occupying river and stream systems on mainland Australia. These studies have revealed that platypuses are typically nocturnal (Grant et al. 1992, Grigg et al. 1992, McLeod 1993, Serena 1994, Gust and Handasyde 1995), a behaviour that is regularly observed in a variety of mammals (Refinetti 2000). According to Cloudsley-Thompson (1965), the nocturnal habit confers several advantages including the avoidance of predators as well as of competition between species, as a result of which vulnerable forms especially tend to forage during night time (Cloudsley-Thompson 1965).

However, variations to this typical nocturnal pattern of platypus activity have been observed by a number of authors. Grant (1992a) and McLeod (1993) consistently report diurnal activity of platypuses, mostly associated with the breeding season or the lactation period in the female. Gust and Handasyde (1995) observed a higher incidence of diurnal activity of platypuses in late winter and spring in the Goulbourn River, Victoria. During the non-breeding season, departure and return times of platypuses were extremely regular and no study animals were observed to be active in daylight hours. Emergence and return times of male platypuses varied substantially during the breeding season with some males changing from nocturnal to diurnal activity pattern (Gust and Handasyde 1995). This change was consistent with a large increase in the number of both male and female platypuses observed to be active during the day. In addition, Serena (1994) reported considerable individual variation in the incidence of diurnal activity at Badger Creek, Victoria. For example, two lactating females were found to emerge from their burrows well before dark in late spring. Adult females were also active during the day in late autumn.

In this study, nearly two thirds of all platypuses examined were mainly active during nighttime confirming that platypuses at Lake Lea, consistent with

other populations, predominantly occupy a nocturnal niche. However, one third of all animals showed 'mixed' activity, which occurred throughout the year. At least two animals showed a distinct shift in activity pattern related to the lunar cycle, which has not been reported in platypuses before (03-98-4 & 12-98-1, see Fig. 4-20 and Fig. 4-21 as well as App. A). This behaviour is normally observed in animals that live close to the ocean and feed in intertidal areas (Wikelski and Hau 1995, Refinetti 2000). In the case of the platypus, however, temporarily following the lunar rhythm might be prey related (Munks, personal communication) or might well act as a mechanism that effectively allows temporal separation between individuals (see Chapter 6.4.13).

Most of the platypuses with irregular activity did not seem to follow a distinct pattern in their activity changes but showed quite erratic variations in emergence and return times. Francis (1999) observed platypuses in captivity and reported a similar unstable zigzag entrainment in one animal. A similar pattern has also been observed in other den-dwelling animals and may reflect light-sampling activity (Decoursey 1986, Decoursey and Menon 1991, Francis 1999). Also, spontaneous switching from diurnal to nocturnal activity modes (or vice-versa) has been observed previously in a variety of mammals (e.g. Stebbins 1971, Johnstone and Zucker 1983).

Strictly diurnal activity was observed in winter in three female platypuses at Lake Lea. These results are consistent with the observations of Otley et al. (2000) who reported a high proportion of daytime activity in female platypuses at Lake Lea, especially in winter. Otley et al. (2000) suggested a higher incidence of diurnal behaviour at Lake Lea compared to habitats on the Australian mainland, but did note that most mainland studies did not quantify the lengths of diurnal activity, with radio tracking mostly restricted to night times only. Serena (1994) provided a quantification of diurnal activity with Badger Creek animals reported to be diurnally active on 8 % of all days located. This figure is indeed much lower than the observed 40 % of individuals regularly performing 'mixed' (i.e. partly diurnal) or strictly diurnal activity at Lake Lea. However, due to different methodology, figures from this and the other studies are not

comparable, and more detailed studies of foraging pattern in mainland and river habitats are recommended.

At Lake Lea, highly variable activity patterns and partly diurnal activity were observed not only in winter and during the breeding season but throughout the year. Strict or partial diurnal behaviour appears to be more common than in the river systems studied so far on the mainland. Foraging duration and emergence and return times of platypuses at Lake Lea varied considerably between individuals in all seasons. Even within the group of diurnal and nocturnal animals, emergence and return times deviated for up to six hours from sunset/sunrise times, respectively (Fig. 6-15). In contrast, Gust and Handasyde (1995) found in the Goulbourn River, Victoria, that typically, platypuses left their burrows within 3 hours after sunset with departure and return times being extremely regular during the non-breeding season. Grant et al. (1992) investigated platypuses in the lower Thredbo River, NSW, over two to five months using radio-telemetry and found that most individuals emerged between 6:15 p.m. and 9 p.m.

It is interesting to note that a considerable flexibility in phase-relations and switching between diurnal and nocturnal modes of activity has also been observed in captive platypuses. Francis (1999) studied three platypuses within the platypussary at the Royal Melbourne Zoological Gardens and observed a mainly nocturnal pattern of activity under controlled and natural light-dark cycles. However, there were scattered activity episodes throughout the day and several days on which activity was recorded throughout most of the light phase. In one animal, Francis (1999) found a considerable variability in phase-relations between activity onset and dusk with a predominantly diurnal pattern over half of the experiment. In the second half of the experiment however (100 days overall for whole experiment) activity was nocturnal.

6.4.12 Social interaction between individuals and spatial separation

In light of these findings it is tempting to speculate about the reasons for the highly variable activity pattern of platypuses at Lake Lea. Temporal activity patterns of animals are reportedly influenced by a number of ecological factors including food and mate competition, predator avoidance, thermoregulation costs and temporal availability of prey (Cloudsley-Thompson 1965). In mammals, female spacing patterns tend to be determined by the abundance and dispersion of food, whereas male arrangement is related more to the distribution of females (Cameron and Spencer 1985, Sandell 1989). Francis (1999) suggested that occasional activity outside of the main nocturnal niche might be a pattern related to the seeking of a mate or resource partitioning. Gust and Handasyde (1995) speculated that diurnal activity might enable male platypuses to avoid aggressive encounters with other males during the breeding season, or that it might be a response to alterations in the temporal distribution of reproductive females (Clutton-Brock 1989).

The results of this study suggest that differences in platypus behaviour at Lake Lea compared to river systems can be attributed to mainly two factors: the harsh climate conditions and the special conditions and limitations connected with a lake habitat in contrast to a river or stream habitat. Studies of other semiaquatic mammals show that differences in behaviour including foraging duration and home range size and arrangement occur between lentic and lotic habitats (Dunstone and Birks 1985, Reid et al. 1994, Kruuk 1995).

Before exploring these factors further, however, it is useful to review the system of social interactions between individual platypuses in order to be able to discuss their implications on activity pattern. The platypus is largely considered a solitary species and apart from the breeding season platypuses rarely interact with each other (Temple-Smith 1973, Grant 1983a, Lamm 1993). However, spatial overlap has been observed in the home ranges between individuals of all ages and gender. In addition, in some studies, social units have been identified (Grant 1992a, Grant et al. 1992) consisting of a group of resident and a number of transient individuals. The latter were found to be predominantly

male and possibly represented the dispersal of subadults (Grant 1992a) ready to take up vacant sites or occupy home ranges from resident males (Gardner and Serena 1995). At Lake Lea, a resident population of 28 animals (13 females, 15 males) was observed over the two year period of field work while 24 transient individuals (5 females, 19 males) stayed temporarily at the Lake (see Chapter 2.2.3). A comparable population pattern is also found in other semiaquatic mammals, including for example the desman (Stone 1987a) and the European otter (Erlinge 1967, Erlinge 1968).

These observations indicate that competition between individuals might play an important role in determining activity pattern of platypuses, and studies in the wild as well as in captivity support this suggestion. Hawkins (1998) monitored platypuses in Taronga Zoo and found that, when alone, the animals linked their activity to the nocturnal light cycle and followed a predictable pattern of activity. However, when individuals were paired, a dominance relationship usually developed (Hawkins 1998). Adult males were dominant over females in all cases. In the combination of a subadult male with a female, the female remained dominant, and between two females, there was little indication of dominance. While the dominant animal's pattern of activity remained similar to that when kept alone, except for a slight lengthening of its active period, the second animal's active period shortened and became more fragmented (Hawkins 1998).

Spatial and temporal separation due to social interactions have also been observed in wild platypuses. Radio-tracking studies by Serena (1994) in southern Victoria showed that adult females are not territorial in the sense of defending mutually exclusive areas and tolerate a great deal of spatial overlap between individuals. Yet, adult males did not tolerate other adult males, an observation also made by Gardner and Serena (1995) who reported that males largely avoided each other, spending most of their time in different parts of the range. Serena (1994) suggested that adult males might occupy and actively defend mutually exclusive home ranges in the study area, presumably in order to monopolise resident breeding females.

The degree of social tolerance, however, reflected by the degree of home range overlap, was found to vary between habitats. While male platypuses engaged in territorial defence in narrow linear systems (Serena 1994, Gardner and Serena 1995), they tolerated more home range overlap in wider rivers and weir systems (McLeod 1993, Gust and Handasyde 1995). Radio-tracking studies undertaken along the Thredbo River, NSW (Grant et al. 1992), and along the Goulburn River, Victoria (Gust and Handasyde 1995), showed that the home ranges also of adult male platypuses overlapped substantially.

Why then do male platypuses fail to maintain territories in larger systems? In theory, the upper limit to territory size is set by the costs of defending an area, as determined by the time and energy required to patrol boundaries and evict trespassers (Brown and Orians 1970, Gardner and Serena 1995). Davies (1978) pointed out that territorial behaviour only exists if the costs in time and energy spent in defence are outweighed by the benefits of exclusive use of an area. To defend an exclusive territory in a relatively narrow water body should be easier than the defence of broader and deeper systems, as more time and energy must be spent patrolling the boundaries (Serena 1994, Otley 1996). In addition, Gust and Handasyde (1995) suggested that home range size and degree of overlap were related to population size and density. While narrow habitats with exclusive platypus territories had population densities of only between one to two individuals per kilometre of waterway (Serena 1994, Gardner and Serena 1995) broader habitats with overlapping home ranges showed much higher population densities (Grant and Carrick 1978, 10 to 12 individuals per kilometre). In such habitats, a point may be reached where area defence is not a viable strategy and overlapping ranges are the result (Brown and Orians 1970, Otley 1996).

Spatial separation of individuals with some degree of overlapping between territories has been suggested to be a typical behaviour for carnivorous semiaquatic mammals that occupy river habitats (Gardner and Serena 1995). Both female and male otters, *Lutra lutra*, for example occupy intra-sexually exclusive territories, with each male typically overlapping the areas of several

females (Erlinge 1967, Erlinge 1968). In contrast, spotted-neck otters, *Lutra maculicollis*, and giant otters, *Pteronura brasiliensis*, both appear to occupy communally defended group territories shared by several adult males and females (Procter 1963, Duplaix 1980). In the case of desmans, *Galemys pyrenaicus*, resident pairs defend a shared territory, with the home range of each male completely enclosing that of his mate (Stone 1987a).

Given these results, what would one expect a platypus to do in a lake system? Otley et al. (2000) pointed out that in an aquatic habitat like Lake Lea, the cost of dominating an area might be increased, given that potential intruders are predicted to be both more numerous and more widely distributed than in the case of a linear system. Also, while there is a much larger foraging area in a lake, there is not a proportional increase in bank area available with the need to share a limited number of suitable burrow sites. During this study more than one (up to three) resident males were captured at one particular trapping site in 12 occasions (see Chapter 6.3.3, Tab. 6-6) indicating a high tolerance of animals in sharing their burrow areas. Females were even more tolerant with up to six resident females sharing the same burrow area. This suggests that platypuses in lakes are not likely to maintain an exclusive territory but that they rather try to avoid intra-specific competition through other measures, including a considerable tolerance in the degree of home range overlap.

The relatively high number of platypuses caught in the lake, a considerably high tolerance of adult males to share burrow sites and the co-existence of platypuses with brown trout (*Salmo trutta*) and water rat (*Hydromys chrysogaster*) at Lake Lea (Bethge, Munks and Otley, personal observations) indicate that the productivity of Lake Lea is likely to be high enough to support a quite large platypus population. We would expect considerable overlap in home ranges at Lake Lea as seen in large linear systems with high population densities (Grant et al. 1992, Gust and Handasyde 1995). Otley (1996) reported a strong preference of platypuses for feeding in the lake rather than in associated streams or remote pools suggesting that there might be a higher prey density and diversity in the lake compared with the other waterways.

6.4.13 Temporal separation

High population densities force animals close together with a reported decrease in home range size (Brown and Orians 1970) and consequently a decrease in resource access for the individual. From a certain degree of population pressure onwards, there is a particularly high adaptive value in possessing the ability to develop strategies, which can reduce intra-specific competition, and a strategy commonly adapted by a number of animals is temporal separation (Cloudsley-Thompson 1980).

The high variability in activity pattern found in this study indicate that temporal separation plays a vital role for social organisation of platypuses at Lake Lea. Mainland studies suggest that temporal separation is used by platypuses only as a last resource if spatial separation is not a viable strategy to reduce competition. Therefore, competition between platypuses at Lake Lea appears to be high and requires additional measures other than spatial separation. Nocturnal and diurnal activity pattern are only two of a number of temporal organisation forms of foraging activity that were observed at Lake Lea. Platypuses showed a broad range of 'mixed' behaviour pattern. Especially the highly developed strategy of temporarily following the lunar rhythm found in at least two animals (03-98-4 and 12-98-1, see Fig. 4-20 and Fig. 4-21, Appendix A) suggests an effective mechanism of temporal separation between individuals. Consistent with these observations, Otley (1996) found a high incidence of temporal separation of platypuses at Lake Lea and suggested that intra-specific competition due to higher population densities at Lake Lea than at mainland sites was the main reason for the temporal partitioning.

The comparison of population densities between lake and river systems is difficult as both habitats show very different physical characteristics. However, Otley et al. (2000) observed platypuses at Lake Lea mainly feeding close to the lake shore with a preference for shallow water, which was confirmed in this study. This suggests that a lake from a platypus' perspective is comparable to a circular stream, as mainly the shore areas seem to be important for foraging. Therefore, Lake Lea with a size of approximately 142 hectare could be de-

scribed as a stream with a length of about 5.7 kilometres. Assuming a resident population of 28 individuals (see Chapter 2.2.3) this yields a population density of only around five individuals 'per kilometre'. Even by adding a considerable number of transient animals, population densities get nowhere near those found in large linear habitats on the mainland with reportedly 10 to 12 individuals per kilometre (Grant and Carrick 1978).

This suggests that a high population pressure might not be the main cause for temporal partitioning at Lake Lea but rather a limitation of suitable burrow sites as well as foraging locations, which, as a consequence, have to be shared by individuals. Male platypuses in particular are not likely to tolerate other individuals in the core area of their territory, which in lake systems is likely to centre around the particular shore area where the burrow site is located (Otley et al. 2000). Indeed, temporal separation between resident male platypuses was observed in at least five cases at Lake Lea (see Chapter 6.3.3, Tab. 6-6). Results suggest that the most dominant male generally shows nocturnal behaviour while lower ranked males adopt 'mixed' activity pattern.

Platypuses are known to forage in direct proximity to their burrow sites at least towards the end of their foraging trips (Gardner and Serena 1995). Therefore, lower ranked animals might choose to avoid emergence and return times of dominant individuals living at the same burrow site. Hawkins (1998) found temporal separation in paired captive platypuses and reported that the activity of the inferior animal moved more into the high light periods. The author concluded that one reason behind the changes of activity pattern in platypuses was the desire for an uninterrupted feeding time.

Hawkins (1998) also reported that activity of an inferior animal became more fragmented and shortened when a dominant animal was present. This could well explain some of the highly irregular activity recorded in platypuses at Lake Lea, especially during the breeding season when dominance is probably marked. The most irregular behaviour observed during this study was shown by a female platypus during the mating season (10-98-4, see App. A). This animal lived in a creek as well as in corresponding pools in the Vale of

Belvoir next to the lake. It showed very erratic changes in emergence and return times as well as fragmented foraging trips. This behaviour in combination with a small creek and pool habitat, where spatial separation is not a viable alternative to temporal partitioning, suggests that this female's activity pattern might well have been influenced by the activity of a dominant male.

A limited number of suitable foraging locations might also contribute to the observed temporal separation of platypuses at Lake Lea. Spatial separation is not a viable strategy for sharing a limited number of prime foraging locations with high productivity. Therefore, temporal separation is used. Accordingly, Otley et al. (2000) found that individuals fed quite regularly in similar areas in the lake, however temporarily separated. A similar preference for specific foraging locations has also been reported by Kruuk (1993) who observed that when several animals were foraging along the same stretch of river they often dived and came up with prey in places which had been previously searched by other platypuses. Therefore, temporal separation of platypuses at Lake Lea might predominantly be a strategy to avoid 'traffic jams' at a limited number of burrow sites and prime foraging locations.

Another hint that temporal separation might relate to a system of dominance in the platypus population at Lake Lea is the fact that six out of the seven platypuses which were equipped twice with data-loggers during this study showed the same activity pattern in both experiments. This suggests that the animals occupy a relatively stable social position in the overall population, which does not allow much variation in their general activity pattern. In this respect, it is interesting to note that the two juvenile platypuses investigated in this study were found to follow very strict nocturnal rhythms (04-98-3 and 04-98-4, see Appendix A). Consistent with this observation, Serena (1994) found three first-year platypuses in autumn/winter to be strictly nocturnal. Also, McLeod (1993) found that while adult emergence and return times were not significantly correlated with sunset and sunrise times, the times of juvenile males were. Home ranges of juvenile as well as subadult platypuses are known to overlap substantially with those of adult individuals, including adult males

(Serena 1994), and competition does not seem to play a role in these cases resulting in a lack of temporal separation.

Possible reasons for temporal separation other than competition for food and mates include thermoregulatory benefits, predator avoidance, inter-specific competition or synchronisation with prey activity. At Lake Lea, the water rat (*Hydromys chrysogaster*) and the brown trout (*Salmo trutta*) are possible food competitors of platypuses. Water rats in particular have similar dietary and burrow requirements (Woollard et al. 1978, Olsen 1983). However, water rats were only rarely observed at Lake Lea. Also, Dawson and Fanning (1981) reported that *Hydromys* cannot maintain its body temperature at water temperatures below 25°C which suggests that the climate at Lake Lea is too harsh for the water rat and prevents the animal from being a permanent resident. Therefore, inter-specific competition is not likely to be an important selective factor in platypus activity pattern at Lake Lea.

Otley (1996) suggested that the lack of many predators and the isolated characteristic of Lake Lea could be a factor explaining and indeed allowing temporal separation between individuals as well as diurnal activity. Temple-Smith (2000) pointed out that the failure of past attempts to introduce red foxes into Tasmania is probably the most important difference in predation pressure between most mainland populations and the Tasmanian platypus population. Temple-Smith (2000) suggested that this might have influenced the extent of diurnal behaviour of Tasmanian platypuses. In addition to a low predation pressure, the level of disturbance by human activity is low at Lake Lea with an estimated 100 anglers per season (Cutler 1992). However, the implications of human activity on platypus behaviour are not thoroughly investigated and might be overestimated by the human observer. Serena et al. (1998) investigated platypuses living in the Melbourne metropolitan region and found that the animals travelled below one- and two-lane bridges on many occasions without appearing to be disturbed by noises or vibrations caused by the traffic.

6.4.14 Seasonal differences in activity pattern

Temporal partitioning of shared areas by vertebrates has previously been postulated to contribute to improved foraging efficiency or to develop as an outcome of aggressive behaviour serving primarily to deter immigration by non-neighbours (Cloudsley-Thompson 1965, Gardner and Serena 1995). Accordingly, temporal separation in male platypuses might also serve as a strategy to prevent transient males from using the lake area, especially during the breeding season. At Lake Lea, 19 transient males were recorded during the two year observation period (see Chapter 2.2.3) with the highest percentage of transient males observed in spring during the mating season (see Fig. 2-8). Correspondingly, daily rhythm was shifted to more irregular activity pattern during the mating season with more than 50 % of all animals showing 'mixed' behaviour (Fig. 6-11).

This observation could also relate to an increase in searching behaviour for mates and, accordingly, an increase in social interaction during the mating season. Grant (1995) noted that males are highly engaged in courtship as well as in defending their territory against competitors in spring. At the same time, females have to build up fat stores for the three months lactation period beginning in late spring/early summer. At Lake Lea, results from the approximate age of juveniles gave the mating season as October to February with young emerging around April/June (Munks et al. 2000). Activity levels of platypuses, however, were highest between August and November (Fig. 6-8). This suggests that mating season at Lake Lea already starts in August (one month later than in lowland habitats, Grant 1995) and lasts until the end of November. Correspondingly, lactation season might be delayed by one month due to the harsh climate conditions at Lake Lea and is suggested to last from November until the end of April (Fig. 6-21).

Otley (1996) reported that at Lake Lea the size of foraging ranges appeared to be influenced by the reproductive status. Larger foraging ranges were observed during the mating season. Also, Gust and Handasyde (1995) reported some temporal separation between adult males during the breeding

season. The authors found greater variation in the times at which animals emerged from their burrows, and some animals became diurnal. Gust and Handasyde (1995) suggested that in addition to spatial separation, temporal spacing of activity patterns might be a mechanism by which some males avoid aggressive encounters with other males. Such behaviour would effectively decrease the number of adult males using the habitat at any one time (Gust and Handasyde 1995).

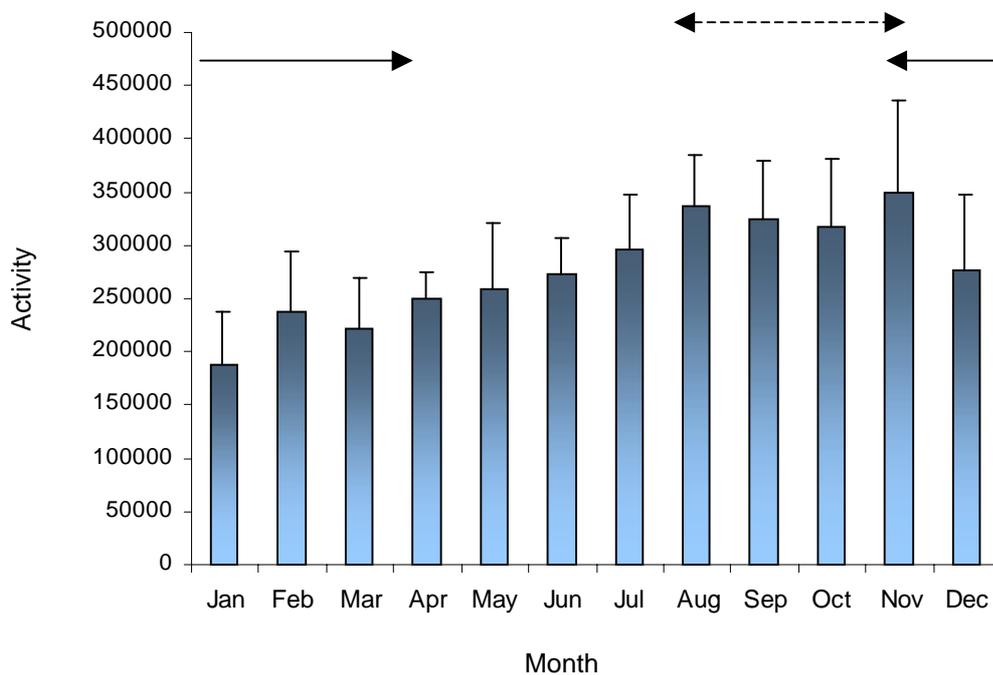


Fig. 6-21: Daily activity over the year of platypuses at Lake Lea and suggested mating (dotted arrow) as well as lactation season (solid arrow). Bars show standard deviations

Activity patterns of platypuses at Lake Lea changed with season. A higher rate of diurnal activity was observed during autumn and especially during the winter months, predominantly in female individuals (Fig. 6-11, Fig. 6-12). Grant (1983a) suggested a winter shift to diurnal activity as a strategy for heat conservation, avoiding times of lowest air temperatures. A number of other small semiaquatic mammals in high northern latitudes are known to reduce thermoregulatory costs during winter in part by becoming more diurnal

(Gerrell 1970, Melquist and Hornocker 1983, Dyck and MacArthur 1992). At Lake Lea, winter is a season of extreme climate conditions. Especially for females with their lower body mass it seems reasonable to shift activity to an energetically more efficient behaviour. Consistent with these findings, Otley et al. (2000) proposed thermoregulation to be the essential factor influencing the high incidence of diurnal behaviour of female platypuses in winter. However, it has to be taken into account that seasonal variation in hours of daylight and darkness is greater at Lake Lea than at mainland study sites. The number of hours spent foraging during light conditions, where higher air temperatures are expected, was actually lower in autumn and winter than in spring and summer at Lake Lea (Fig. 6-14).

7 *Platypus* burrow temperatures

7.1 Introduction and Methods

When platypuses are not in the water, the microhabitat of their burrows is of great importance for energy conservation, especially in harsh habitats like Lake Lea, where air temperatures frequently fall below freezing in winter (Grant 1983a). In this study, the use of time-depth recorders with integrated temperature sensors made it possible to determine burrow temperatures of platypuses in the wild. Information on burrow temperatures was obtained from nine individual platypuses.

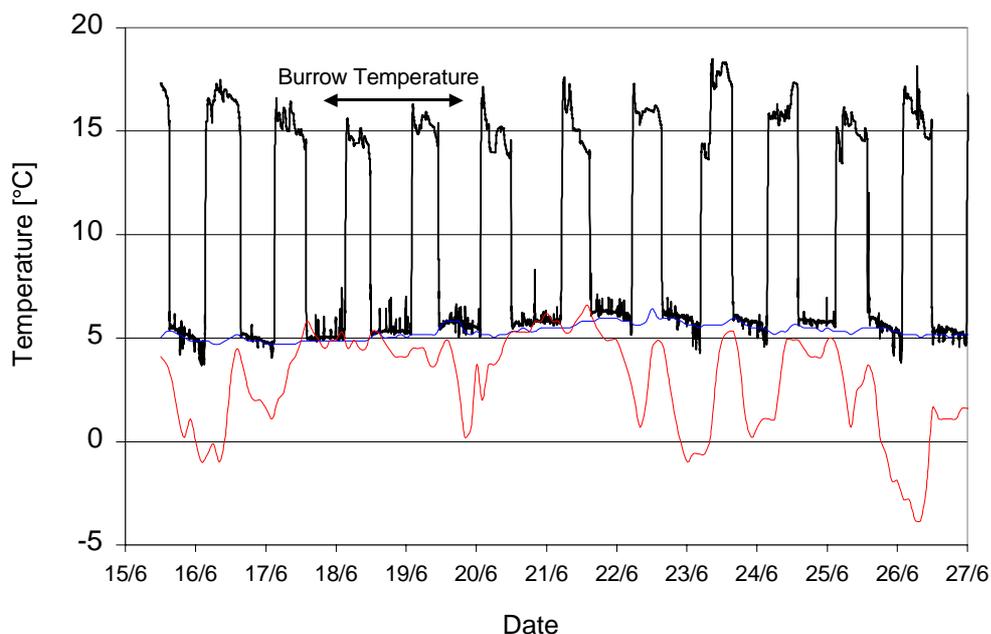


Fig. 7-1: Sample data of water (blue line), air (red line) and TDR-temperatures (black line, derived from a time-depth recorder fitted to the back of a male platypus (06-99-2) at Lake Lea in winter)

All investigated platypuses occupied burrows in consolidated steep or gently sloping earth banks of the lake or along associated creeks at sites 3, 6, 7 and 9 (Fig. 2-3). Temperature sensors were located at the back end of the de-

vices (see Appendix C) and were facing backwards when the devices were fixed on the platypus's lower backs. While foraging, the sensors measured water temperatures. In resting platypuses, ambient temperatures close to the animals' body (approx. 5 mm from above the fur) were recorded. A sample of measured TDR-temperature and corresponding air and water temperature is shown in Fig. 7-1. All temperature data-files are shown in Appendix A together with the dive profiles of the corresponding animals.

7.2 Results

Burrow temperatures, i.e. ambient temperatures during resting periods, were recorded in two hour intervals for a total of 61 resting periods from nine individual platypuses and were averaged over the period of resting. Resting periods ranged from 5.45 to 27.20 hours. Mean burrow temperature was 17.5 and 14.2°C (SD=2.76 and 0.89, respectively, n=9) in summer and winter, respectively, and ranged between 12.2 and 22.8°C for individual resting periods. In winter, burrow temperature was held fairly constant over the resting period while in summer larger variations were observed (01-00-1, 02-99-2, 12-99-2, see Appendix A). In winter, burrow temperature was found to be up to 18°C higher than air temperature (Fig. 7-1). A low but significant correlation between air temperature and burrow temperature was found with higher air temperatures resulting in higher burrow temperatures (Fig. 7-2, coefficient=0.19, constant=14.94, $r^2=0.136$, $p=0.003$, $n=61$).

7.3 Discussion

Grant (1983a) found that even in an unoccupied artificial burrow the insulation of layers of earth provided a significant buffering effect against outside ambient temperature changes in both winter and summer. In winter, unoccupied burrow temperatures in the upper Shoalhaven River, NSW, averaged around 14°C despite the fact that ambient air temperatures dropped as low as -5°C. During summer the temperature of unoccupied burrows averaged around

18°C with air and water temperatures being several degrees higher (Grant 1976, Grant 1995). In addition, from data collected with temperature transmitters, Grant (1983a) suggested that the animals' presence further elevates the microhabitat temperature of the burrow.

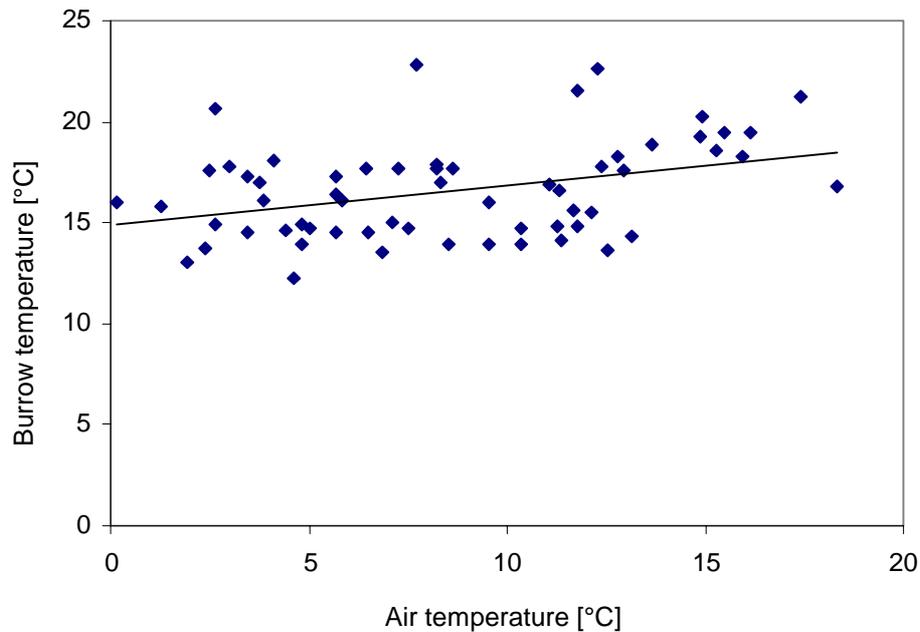


Fig. 7-2: The relationship between air temperature and burrow temperature (measured on the back of platypuses at Lake Lea). Solid line shows regression ($r^2=0.136$, $p=0.003$, $n=61$)

Surprisingly however, findings presented here from occupied burrow sites are in line with temperatures measured by Grant (1976) from unoccupied burrow sites. This suggests that temperature in platypus burrows is mainly determined by physical characteristics of the burrow site rather than by metabolic heat produced by the animal. The excellent insulation of the platypus body (Grant and Dawson 1978b) seems to greatly restrict heat loss of the animal not only in water but also in the burrow. In winter, this is an advantage, as low ambient temperatures do not cause a risk of life threatening heat loss. In summer, however, high ambient temperatures are likely to pose a threat at platypuses due to the lack of an effective cooling mechanism (Grant and Dawson 1978a).

All burrow temperatures in this study were measured in burrows located in consolidated earth banks. However, Otley et al. (2000) reported that 25 % of burrows at Lake Lea were located above ground within dense vegetation, such as sphagnum and button grass. This percentage is much higher than that reported in mainland studies, where only a 5 % incidence of burrows in non-earth structures was found (McLeod 1993, Serena 1994). Otley et al. (2000) suggested that burrow sites in steep earth banks, previously reported as platypus prime burrow sites (McLeod 1993, Gust and Handasyde 1995, Grant 1995, Serena et al. 1998), may be limited at Lake Lea forcing platypuses to use alternative burrow locations. In respect to burrow temperatures, a burrow above ground within vegetation would have worse insulation properties than an underground burrow. How animals cope with low and high ambient temperatures in such a vegetation burrow and if they use this sort of burrow site regardless of season requires further investigation.

8 Metabolic rates of free-living platypuses

8.1 Introduction and methods

To date, studies on the energetic demands of platypuses in the field are rare and rely mostly on calculations of time energy budgets on the basis of resting metabolic rates (Grant and Carrick 1978, Faragher et al. 1979). Only recently, Munks et al. (2000 and unpublished data) calculated field metabolic rates using the doubly-labelled water method.

In this study, daily energy requirements of platypuses were derived through the calculation of time-energy budgets on the base of both field and laboratory data. Field metabolic rates were estimated for 29 individual platypuses using data from 824 foraging trips, which were recorded by both types of data-loggers. To translate both activity profiles and dive profiles into energy consumption, Equations (1), (2) and (3) obtained in the swim tank experiments (Chapters 4.3.1 & 4.3.2) were used:

$$P_{(\text{REST})[\text{in air}]} = 0.035 T_a + 24.49 T_a^{-1} + 0.3 \quad (1)$$

$$P_{(\text{REST})[\text{in water}]} = 0.107 T_w + 61.77 T_{a/w}^{-1} - 1.48 \quad (2)$$

where $T_{a/w}$ = air/water temperature [°C] and $P_{(\text{REST})}$ is in W kg^{-1} ;

$$P_{(\text{FORAGE})} = 9.04 - 0.21 T_w - 0.90 m + 109.21 t^{-1} \quad (3)$$

(in W kg^{-1}) where T_w = current water temperature [°C], m = body mass [kg] and t = dive duration [s]. For reasons discussed earlier (Chapter 4.4.1), foraging costs derived in the swim tank (Equation 3) are likely to underestimate the power requirements of platypuses foraging in the wild. Therefore, field metabolic rates derived in this section are clearly minimum rates accordingly labelled $\text{FMR}_{(\text{MIN})}$.

Dependent on logger type, different methods were applied to calculate energy consumption during foraging. Dive profiles obtained with the time-depth recorders were directly translated into energetic costs using Equation (2)

and (3). Costs for each dive and each inter-dive foraging break were calculated. Energetic costs for each foraging trip were then summed to yield the total costs for the foraging trip $C_{(TRIP)}$ [$J\ kg^{-1}$].

To translate the activity profiles derived from activity loggers into energy consumption, activity sensors were calibrated in the swim tank as well as in the wild. Three animals in the wild and six animals in the swim tank were equipped with activity loggers (AL) running with fast sampling-interval (2 s). These files showed subsequent bursts of activity which resembled diving activity recorded with the time-depth recorders (sample data see Fig. 6-2.). No activity was recorded during inter-dive surface periods. The response of the devices to various dive durations was examined and a strong relationship between activity and dive duration was found (Fig. 8-1, coefficient = 9.9, constant = -32.31, $r^2=0.713$, $p<0.001$, $n=1506$, see App. B-2).

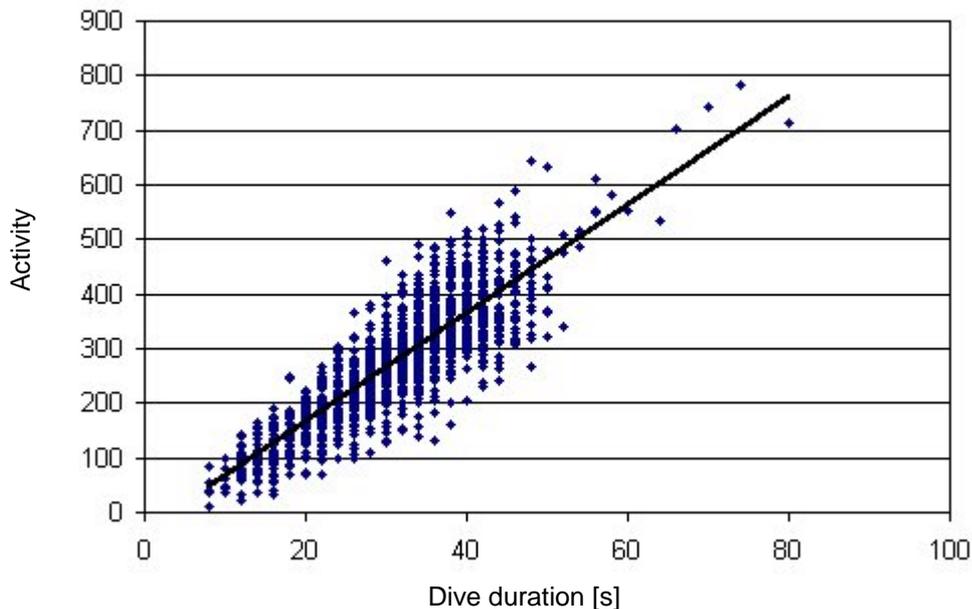


Fig. 8-1: Activity logger calibration: The relation between activity and dive duration. Solid line shows regression ($r^2=0.713$, $p<0.001$, $n=1506$)

Activity was then translated into energy consumption by assuming the AL-foraging trips to follow a similar pattern to that observed in platypuses

equipped with time-depth recorders. Foraging behaviour in platypuses equipped with TDRs was characterised by continuous diving activity. Mean dive duration ($t_{(AV-DIVE)}$) was 31.3 seconds (Chapter 6.3.1). Using the calibration-regression above and Equation (3), this average dive duration can be directly translated into a corresponding activity ($Activity_{(AV-DIVE)}=270$) as well as into corresponding energetic costs (dependant on water temperature and body mass, Equation 3). Assuming that the activity recorded during a foraging trip was mainly caused by diving activity, the number of average dives ($n_{(AV-DIVE)}$) the animal performed during the trip was estimated by following $n_{(AV-DIVE)} = (Activity_{(TOTAL)} / Activity_{(AV-DIVE)})$ where $Activity_{(TOTAL)}$ is the total activity during the foraging trip and $Activity_{(AV-DIVE)}$ ($=270$) is the activity during an average dive of duration $t_{(AV-DIVE)}$ ($=31.3$ s). Consequently, $C_{(TRIP)}$ [$J\ kg^{-1}$] was calculated following

$$C_{(TRIP)} = P_{(FORAGE)} t_{(AV-DIVE)} n_{(AV-DIVE)} + P_{(REST)[in\ water]} t_{(REST)[in\ water]}$$

where $n_{(AV-DIVE)}$ is the total number of dives with the duration $t_{(AV-DIVE)}$ ($=31.3$ s) and $t_{(REST)[in\ water]}$ is the total time the platypus was resting on the water surface during the foraging trip. The latter time was estimated following $t_{(REST)[in\ water]} = t_{(TRIP)} - t_{(AV-DIVE)} n_{(AV-DIVE)}$ where $t_{(TRIP)}$ is the overall duration of the foraging trip.

Energetic costs for inactive periods of the day ($C_{(LAND)}$ [$J\ kg^{-1}$]), i.e. resting periods presumably in the burrow, were calculated using Equation (1). Air temperatures were substituted with the burrow temperatures derived from time-depth recorders (see Chapter 7).

Minimum field metabolic rates for each 24-h period (in [$J\ kg^{-1}\ day^{-1}$]) were then obtained following $FMR_{(MIN)} = C_{(TRIP)} + C_{(LAND)}$.

8.2 Results

For each foraging trip, minimum field metabolic rates ($FMR_{(MIN)}$), foraging costs ($C_{(TRIP)}$, i.e. the costs for a whole foraging trip in kJ kg^{-1}) and foraging rates ($P_{(TRIP)}$ in W kg^{-1}) were calculated. $FMR_{(MIN)}$ estimated from TDR measurements ranged from 235 to $790 \text{ kJ kg}^{-1}\text{day}^{-1}$ while $FMR_{(MIN)}$ estimated from AL measurements ranged from 264 to $909 \text{ kJ kg}^{-1}\text{day}^{-1}$. In summer data, no significant differences between the two data sets were found for field metabolic rates and foraging costs (t-tests, $t=0.403$, $P=0.688$ and $t=-0.767$, $p=0.444$, respectively). However, summer foraging rates were significantly different between logger types (t-test, $t=3.933$, $p<0.001$). In winter data, both field metabolic rates and foraging costs were significantly different between logger types (t-test, $t=-4.896$, $p<0.001$ and $t=-5.275$, $p<0.001$, respectively). However, in winter data no significant differences in foraging rates were found (t-test, $t=-0.363$, $p=0.717$). In summary, although differences between the two data sets were small, data collected with time-depth recorders and activity loggers were analysed separately. Results are summarised in Tab. 8-2.

Season	Device	n	$C_{(TRIP)}$		$P_{(TRIP)}$		$C_{(LAND)}$		$FMR_{(MIN)}$	
			$[\text{kJ kg}^{-1}]$	(SD)	$[\text{W kg}^{-1}]$	(SD)	$[\text{kJ kg}^{-1}]$	(SD)	$[\text{kJ kg}^{-1}\text{day}^{-1}]$	(SD)
Spring	AL	40	388.86	(72.94)	7.91	(0.83)	88.33	(21.57)	477.19	(57.00)
Summer	AL	258	289.28	(81.24)	6.23	(0.84)	91.17	(26.45)	380.44	(55.02)
	TDR	66	280.80	(75.36)	6.66	(0.62)	102.63	(28.97)	383.43	(48.76)
Autumn	AL	163	413.50	(104.79)	8.13	(0.94)	84.68	(24.85)	498.18	(82.22)
Winter	AL	265	541.10	(95.01)	10.56	(0.92)	85.24	(16.87)	626.34	(81.07)
	TDR	32	446.06	(106.40)	10.50	(0.81)	105.59	(23.11)	551.64	(85.24)

Tab. 8-1: Seasonal foraging costs $C_{(TRIP)}$, foraging rates $P_{(TRIP)}$, costs for resting $C_{(LAND)}$ and minimum field metabolic rates $FMR_{(MIN)}$ of platypuses at Lake Lea (AL=activity logger, TDR=time-depth recorder).

In data derived from both logger types, minimum field metabolic rates were dependant on season (ANOVAs, $p<0.001$ for both data-sets, see Appendix B-2) with higher rates in winter than in summer and intermediate rates in

spring and autumn (spring and autumn data derived from activity loggers only). No significant differences were found between spring and autumn field metabolic rates ($p=0.348$). Accordingly, a strong relationship between water temperature and field metabolic rate was observed with higher water temperatures causing lower field metabolic rates (ANOVA, $p<0.001$, see App. B-2).

$FMR_{(MIN)}$ was not found to be significantly dependant on air temperature (Multiple regression, $p=0.751$, see App. B-2). Not surprisingly however, a significant effect of foraging duration on $FMR_{(MIN)}$ was found ($p<0.001$). Also, $FMR_{(MIN)}$ was significantly dependent on cloud cover ($p<0.001$) but not on the degree of rainfall ($p=0.367$, see App. B-2)

No consistent results were found regarding the dependency of field metabolic rates on the sex of the platypuses. In data derived from time-depth recorders in summer (t-test, $t=3.122$, $p=0.003$) and in data derived from activity loggers in winter (t-test, $t=-2.663$, $p=0.008$) foraging rates $P_{(TRIP)}$ were significantly different between the sexes. In both cases, female platypuses used significantly more energy per kilogram body mass than male platypuses. However, in winter-data derived from time-depth recorders and summer-data derived from activity loggers no differences between the sexes were found.

8.3 Discussion

8.3.1 Field metabolic rates

Field metabolic rates were obtained using data from two different data-logger types and it is pleasing that both methods yielded nearly the same results for daily energy consumption (Tab. 8-1). However, for reasons discussed earlier, the calculated field metabolic rates most likely underestimate the metabolic needs of platypuses in the wild because they are based on the metabolic rates derived from the swim tank experiments (see Chapters 4.4.1 & 6.4.8). Therefore, field metabolic rates shown in Tab. 8-1 must be regarded as minimum values (accordingly labelled $FMR_{(MIN)}$). To provide a better estimate of the energy requirements of platypuses in the wild FMR-data were corrected

according to the conclusions made earlier while discussing aerobic dive limits of platypuses. Based on data on dive and surface durations of platypuses at Lake Lea, foraging rates derived in the swim tank were found to underestimate foraging rates in the wild by 48 % (Chapter 6.4.8). Correction of pooled FMR-data yields field metabolic rates ranging between 307 and 1306 kJ kg⁻¹ day⁻¹. Mean field metabolic rate was 684.4 kJ kg⁻¹ day⁻¹ (SD=190.9, n=29). Mean field metabolic rate for male and female platypuses at Lake Lea (body mass 2.10 and 1.45 kg, respectively) was 1396 and 992 kJ kg⁻¹ day⁻¹, respectively. Results for different seasons are summarised in Tab. 8-2 and Fig. 8-2.

	<i>FMR min.</i>	<i>FMR</i>	<i>Male</i>	<i>FR</i>	<i>Female</i>	<i>FR</i>
	[kJ kg ⁻¹ day ⁻¹]		[kJ day ⁻¹]	[g day ⁻¹]	[kJ day ⁻¹]	[g day ⁻¹]
Season						
Spring	477	660	1386	267	957	184
Summer	382	515	1082	208	747	144
Autumn	498	692	1454	280	1004	193
Winter	589	868	1822	350	1258	242
Mean	494	684	1437	276	992	191
		(307 to 1306)				
Faragher et al. (1979)	246 to 371					
Munks et al. (2000)	863 to 1098					

Tab. 8-2: Seasonal field metabolic rates (FMR) and feeding rates (FR, g freshmatter per day) of platypuses at Lake Lea and comparison with other studies (mean body mass for male and female platypuses at Lake Lea was 2.10 and 1.45 kg, respectively)

Faragher et al. (1979) calculated the energy consumption of platypuses spending various lengths of time in the water and in their burrows in both winter and summer conditions using resting metabolic rates and environmental data provided by Grant (1976). In this study, field metabolic rates ranged from 369 to 465 kJ day⁻¹ and from 428 to 557 kJ day⁻¹ for an animal with a body mass of 1.5 kg in summer and winter, respectively. However, energy requirements reported by Faragher et al. (1979) were calculated from metabolic de-

terminations made on resting and quietly swimming animals and it is obvious that they underestimate energy demands of platypuses in the wild (Grant 1976).

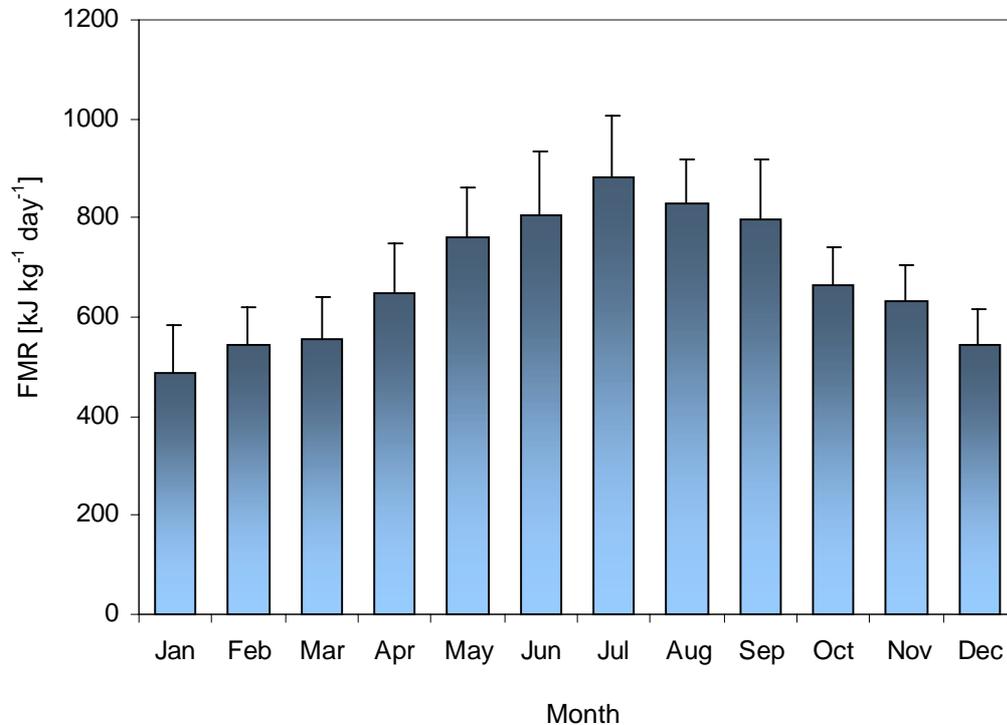


Fig. 8-2: Seasonal field metabolic rates of platypuses at Lake Lea derived from pooled activity logger and time-depth recorder data from the wild in combination with metabolic rates measured in the laboratory. Bars show standard deviations

A direct comparison with the results of this study may be made with the data of Munks et al. (2000) who investigated platypus field metabolic rates at Lake Lea using the doubly-labelled water method. Munks et al. (2000) presented field metabolic rates of 14 individual platypuses and found them to range from 863 to 1098 kJ kg⁻¹ day⁻¹, which is on average around 30 % higher than the results of this study (mean 684 kJ kg⁻¹ day⁻¹, see Tab. 8-2). Differences in methodology are likely to account for the different results. The doubly-labelled water method allows measurement of energy consumption directly in the wild while values obtained in this study base on metabolic rates derived in the laboratory (see also Chapter 9.1).

Field metabolic rates for platypuses at Lake Lea were found to depend on a variety of variables in this study, including foraging duration, water temperature and season, with highest metabolic rates in winter, lowest in summer and intermediate field metabolic rates in spring and autumn (see Tab. 8-2). Consistent with these findings, Faragher et al. (1979) noted that energy expenditure and therefore food requirements of platypuses increased with length of time spent in the water. In addition, Faragher et al. (1979) found that energy expenditure in winter conditions was 16 to 20 % higher than those calculated for summer conditions. The authors suggested that this would force animals to spend more time foraging in winter than in other seasons, a conclusion that was confirmed in this study (see Chapter 6.4.9). Metabolic rates for platypuses in winter presented here were up to 70 % higher than summer values, probably due to the very low winter temperatures at Lake Lea. Munks et al. (2000) also reported a significant increase in energy expenditure of males in autumn/winter. Females showed no significant difference in seasonal energy expenditure in the data of Munks et al. (2000). However, their condition dropped significantly in autumn and winter as indicated by the percentage of total body water.

8.3.2 Platypus food requirements and catch per dive

Grant and Carrick (1978) reported that the number of platypuses occurring in a waterway is determined by the secondary productivity of that waterway, specifically the benthic productivity. The amount of food the animal must eat to provide the energy it uses can be calculated by dividing its FMR by the metabolisable energy content of its food (Nagy 1987). Metabolisable energy in a diet is the gross energy in a unit of food consumed minus the energy lost as faeces and urine resulting from that unit of food.

The platypus is an opportunistic carnivore, eating mainly insect larvae. Following Faragher et al. (1979), the metabolisable energy content of a mixed insect diet was calculated using calorific equivalents from Hawkins and Jewell (1962) and assuming a digestibility of 80 percent. This calculation yields a me-

tabolisable energy content of 5.2 kJ per gram wet weight of mixed insect diet. The daily feeding rate of platypuses at Lake Lea was derived by dividing field metabolic rates by this value. Food requirements averaged 131.6 g freshmatter $\text{kg}^{-1} \text{day}^{-1}$ (SD=35.6, n=35) or 13.2 % of body mass. For an average male (2.10 kg) and female (1.45 kg) platypus at Lake Lea mean daily food requirements accordingly amount to 276 and 191 g freshmatter, respectively (see Tab. 8-2). In winter, food requirements raised to a maximum of 350 and 242 g freshmatter per day for male and female platypuses, respectively. Winter feeding rates were 68 % higher than food requirements in summer (see Tab. 8-2). Munks et al. (2000) estimated a comparable mean food intake of 188 g freshmatter $\text{kg}^{-1} \text{day}^{-1}$ (SD=47.4, n=14) or 19 % of body mass. In the swim tank, platypuses were observed to eat a mean 115 g food $\text{kg}^{-1} \text{day}^{-1}$ (see Chapter 3.4), a value that was expected to be lower than food requirements in the wild.

Platypuses at Lake Lea performed an average of 850 dives per foraging trip (Chapter 6.3.2). Bottom times, i.e. the time for prey search behaviour, averaged around 6.5 hours per day. Consequently, to cover their daily food needs, male and female platypuses at Lake Lea would have to catch 0.32 and 0.22 g freshmatter per dive, respectively, or, as a rule of thumb, one gram of food per two minutes bottom time.

8.3.3 Comparison with other semiaquatic mammals

Nagy (1987) found that metabolic rates are closely correlated with body mass in eutherians, marsupials and birds and derived allometric equations predicting field metabolic rates of free-living mammals. For an eutherian with a body mass of 2.10 kg and 1.45 kg (mean body weights of male and female platypuses at Lake Lea, respectively), Nagy (1987) predicted field metabolic rates of 1683 and 1245 kJ day^{-1} for eutherians as well as 967 and 781 kJ day^{-1} for marsupials. Field metabolic rates of platypuses were found to be intermediate (see Tab. 8-2). This result comes as a surprise because metabolic rates of monotremes are reportedly lower compared to those of most marsupial and

eutherian mammals (Dawson and Hulbert 1970, Grant and Dawson 1978a). However, semiaquatic animals typically show active and inactive metabolic rates that are higher than those of terrestrial species of comparable body size (see Chapter 4.4.2, Irving 1973). These higher energetic costs seem to make up for the energetic advantages the platypus might experience through its monotreme origin.

Consistent with results on transport costs for walking and subsurface swimming, platypus field metabolic rates were in line with those reported for semiaquatic eutherians. Campbell et al. (1998) estimated assimilated energy rates for free-ranging muskrats (*Ondatra zibethicus*) in Canada to average $490.8 \text{ kJ day}^{-1}$ (mean body mass: 0.79 kg). Nolet and Kruuk (1994) estimated net energy intake of a river otter (*Lutra lutra*, body mass 5.4 kg) in Shetland to be 5508 kJ day^{-1} . Based on this data an allometric expression, $\text{FMR} (\text{kJ day}^{-1}) = 634.49 \text{ mass}^{1.262}$ ($r^2=0.99$, $n=3$), was derived (Fig. 8-3).

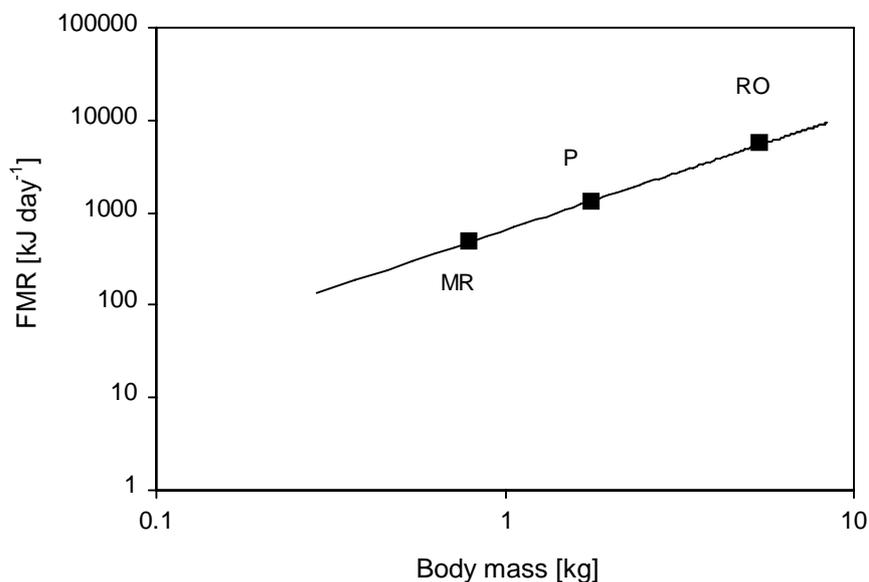


Fig. 8-3: Field metabolic rates of different semiaquatic mammals plotted as a function of body mass (log/log plot). Data on muskrats (MR) from Campbell et al. (1998) and on river otters (RO) from Nolet and Kruuk (1994). Data on platypuses (P) from this study. Solid line shows model for FMR in semiaquatic mammals

However, the exponent of the derived expression is higher than one, which is in contrast to scaling of metabolic rates in mammals generally (e.g. Schmidt-Nielsen 1984). Nolet and Kruuk (1994) investigated one lactating female river otter only, which might explain this unexpected result. Yet, even if the field metabolic rate of river otters in general was overestimated by Nolet and Kruuk (1994), energetic demands of the platypus still remain comparable to those of their eutherian counterparts. To clarify the allometric relation between field metabolic rate and body mass in semiaquatic species, further research into field metabolic rates of mink, muskrat or otter species is strongly indicated.

9 Conclusions

9.1 Time-energy budget and comparison of methodologies

The methods used in this study proved useful for creating a time-energy budget for the platypus. By combining behavioural data with metabolic rates obtained in the swim tank, daily energy needs of platypuses in the wild as well as seasonal field metabolic rates were obtained. Compared to this method, other approaches to estimate energy needs of free-living animals have a number of disadvantages. The doubly-labelled water technique for example, although successfully applied in numerous experiments with aquatic animals in the past (e.g. Gales and Green 1990, Culik and Wilson 1992, Nagy and Obst 1992), has a poor time resolution and sometimes problems with unknown experimental conditions such as the contribution of food and drinking to water exchange rates or unknown activity levels of the studied animals (Nagy 1980, Nagy and Costa 1980, Hull 1997). When used alone this procedure only provides a single value that represents the total food or energy consumption summed over the entire measurement interval (Costa 1988). Heart rate techniques (e.g. Butler and Woakes 1984) offer a better time resolution but pose great challenges to the researchers regarding calibration procedures and require surgery in most cases.

In contrast, creating a time-energy budget for an animal provides a good time resolution and allows partitioning of the various energetic components of the foraging interval (Costa 1988). At the same time, additional behavioural data can be collected which is useful for concurrent studies. However, the limitations of the method should be noted. Creation of a time-energy budget includes the determination of metabolic rates in the laboratory. As seen in this study, this approach has a number of disadvantages. In the swim tank, although voluntary behaviour was possible, animals were put under unnatural conditions, their movements and diving pattern being limited. Consequently, energetic costs derived from laboratory experiments can underestimate the power requirements of platypuses foraging in the wild.

In addition, the partitioning of activity in different behaviours in the wild by the use of data-loggers has its limitations. Depth profiles obtained in this study only allowed the calculation of total diving metabolism regardless of environmental impacts and other aspects of activity. Activity loggers recorded a more complete picture of activity levels in the wild including movement caused by behaviours other than foraging, e.g. walking, burrowing, fighting or courtship and mating behaviour. It was not possible to distinguish between these behaviours and the creation of a time-energy budget in this study relies on the assumption that most activity measured was caused by diving behaviour. However, depth-profiles indicate that indeed platypuses spend most of their active time foraging.

In summary, both time-depth recorder and activity logger data collected in this study are likely to provide a valuable estimate of platypus activity in the wild. After correction on the basis of behavioural data, the derived field metabolic rates as well as platypus food requirements were comparable to values obtained by Munks et al. (2000) using the doubly-labelled water method. In combination with productivity data of lake or river systems, it is my hope that information provided here will help to assess foraging demands of platypuses as well as habitat quality in different environments and thus will be useful for future conservation and management of the species.

9.2 Activity pattern of free-living platypuses

Consistent with results on their energetic demands, 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 due to a merely static ratio between bottom and dive cycle duration. Dive durations as well as surface durations

consequently increased with dive depth, which was found to be the main factor influencing dive cycle organization. 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, aerobic dive limit is exceeded more frequently during the cold season. To cope with the increased metabolic demands in winter, foraging duration is extended and, in some cases, activity is shifted to diurnality. No evidence of torpor or hibernation was observed. Total bottom duration or, if unavailable, foraging duration per day was proposed as a useful indicator of foraging efficiency in the species.

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. River otter and European otter for example have dive durations of 25 seconds and between 13 to 23 seconds, respectively (Conroy and Jenkins 1986, Kruuk 1995). Mink show an average dive time of only nine seconds (Dunstone and O'Connor 1979). 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 seconds for the platypus. However, this study suggests that the unexpected long dive durations of platypuses recorded in the wild are explained by the low energetic costs for diving and consequently the relatively high aerobic dive limit. However, maximum dive times of platypuses are likely to be shorter than previously reported.

Activity patterns of platypuses at Lake Lea were highly variable and considerably different from those observed in linear systems. A high flexibility and lability in the phasing of the circadian pacemaker to the prevailing light-dark cycles was observed with a high percentage of irregular activity patterns. Daily emergence and return times as well as daily foraging trip durations varied considerably. Some animals followed a lunar rhythm in their activity pattern while others foraged for up to 30 hours in some cases. Differences in behaviour compared to linear river systems can mainly be attributed to the harsh climate conditions and the special conditions and limitations of a lake habitat. Temporal

separation was found to play a vital role for social organization of platypuses at Lake Lea. It was suggested that high intra-specific competition as well as a limitation of burrow sites and perhaps of at the same time highly productive foraging locations is mainly responsible for this observation. Some evidence suggests that dominant males are preferentially nocturnal while lower ranked males adopt more variable or fragmented activity patterns. However, results obtained at Lake Lea can not be generalised and comparable research into the behavioural ecology of platypuses in linear systems and in other climate zones is indicated.

9.3 Energetics of the platypus

Energetic demands of the platypus showed the typical characteristics of semiaquatic mammals. Active and inactive metabolic rates were higher than those of terrestrial species of comparable body size. As might be expected for their position between terrestrial and aquatic specialists, the diving platypus was clearly more efficient than surface paddling homeotherms but had higher energy requirements for under water locomotion than specialised divers. Also, energy demands of platypuses while walking were higher than those of terrestrial specialists.

In order to utilise both aquatic and terrestrial environments platypuses require two very different modes of locomotion. Williams (1998) suggested that the transitional lifestyle of semiaquatic mammals incurs costs that are 2.4 to 5.1 times higher than those of locomotor specialists. Results presented here confirm these findings. With increased specialisation of one locomotor mode, a subsequent reduction in locomotor agility of alternate modes occurs (Williams 1983a). Consequently, foraging is preferentially limited to a single habitat, which, in case of the platypus, is clearly the aquatic environment where foraging occurs and food is collected. Minimum transport costs for the walking platypus were found to be 30 % higher than minimum transport costs for sub-

merged swimming. This indicates better locomotor adaptations for the aquatic than for the terrestrial environment.

Compared to eutherian mammals of comparable body size and lifestyle, however, power requirements of the platypus were low. Active metabolic rates in water at preferred speed as well as walking and maintenance costs of the platypus were on average only half as high as those of semiaquatic eutherians - energetic advantages the platypus possibly experiences because of its monotreme origin.

Surprisingly however, transport costs of the animal, i.e. the degree of aquatic specialisation was found to be comparable to that of for example otter and mink. Low locomotor speeds, a small body size, the lifestyle of the platypus and, in the case of walking, possible evolutionary constraints of the monotreme skeletal morphology are likely reasons for this apparent contradiction. While foraging under water, the animal has to optimise for bottom time rather than for speed and therefore efficiency of locomotion. Low metabolic rates while diving enable the animal to stay under water for extended periods in search of food. Optimising the time spent under water rather than the efficiency of locomotion seems ecologically reasonable when the feeding and foraging habits of the animal are taken into account.

Comparable minimum costs of transport of the platypus and its eutherian counterparts might also indicate a general limitation in the efficiency of locomotion in semiaquatic mammals. Even with a generally lower metabolism, the platypus seems to encounter energetic problems during swimming which are comparable to those of its eutherian counterparts. This suggests that, confronted with the need to perform in water and on land, locomotor efficiency of semiaquatic animals might have reached an evolutionary limit for energetic optimisation due to limits in the mechanics of locomotion. Reports on daily energy needs of semiaquatic mammals in the wild are consistent with this suggestion. Field metabolic rates reported for semiaquatic eutherians are in line with those found for the platypus in this study.

A comparable limitation of energetic optimisation was proposed for specialised mammalian divers and runners by Williams (1998) who argued that mammals had to vault an energetic hurdle encountered during the semiaquatic state in the evolution from terrestrial specialists to aquatic specialists. This study supports the view that this energetic hurdle is still challenging today's semiaquatic mammals. The very different physical conditions in the two media land and water impose the same increased energetic demands on semiaquatic mammals regardless of their taxonomic origin.



Photo 9-1: The platypus *Ornithorhynchus anatinus*

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Appendix A: Field data, Actograms**Legend:**

Identity:	file number, sex, status, Tag-No., resident/transient at Lake Lea
Season	season
Activity pattern	activity pattern, circadian period (derived from chi-square periodogram)
Site Type	Creek/Lake-animal (capture site 1 → capture site 2)
Details	Weight, Tail fat, Bill: width/length/length+shield, Body Length, Spur Class, Moulting Class (see below)
Data logger	Logger No. (AW xxxxxx = activity logger, TDR xxxx = time-depth recorder)
Repeat	another file from the same animal? yes/no, file number (logger type)

Platypus Classification:

Tail fat, Tail Volume Index TVI (Grant and Carrick 1978):

The categories, in order from most to least fat, were:

1. Tail turgid with the ventral side convex.
2. Tail able to be folded slightly at lateral edges. Ventral side flat. Rest of tail turgid.
3. Lateral edges of tail easily rolled. Ventral side slightly concave. Rest turgid.
4. Whole tail able to be folded along ventral midline. Whole tail soft.
5. Vertebrae showing through tissue on ventral side. Whole tail soft.

Spur Class (Temple-Smith 1973):

A – Juvenile 0-6 months (both male and female)

B & C – Juvenile 6-9 months (outer horny sheath of spur disintegrating)

D – Subadult male 9-12 months

E – Adult male 12+ months

F – Old adult male (spur may be worn down)

0 – Adult female, no spurs

Moulting Class (Grant and Carrick 1978):

none – guard hairs of pelage intact

very light – small groups of guard hairs missing. Noticeable only on dry animal

light – patches of guard hair missing. Often noticeable only on dry animal

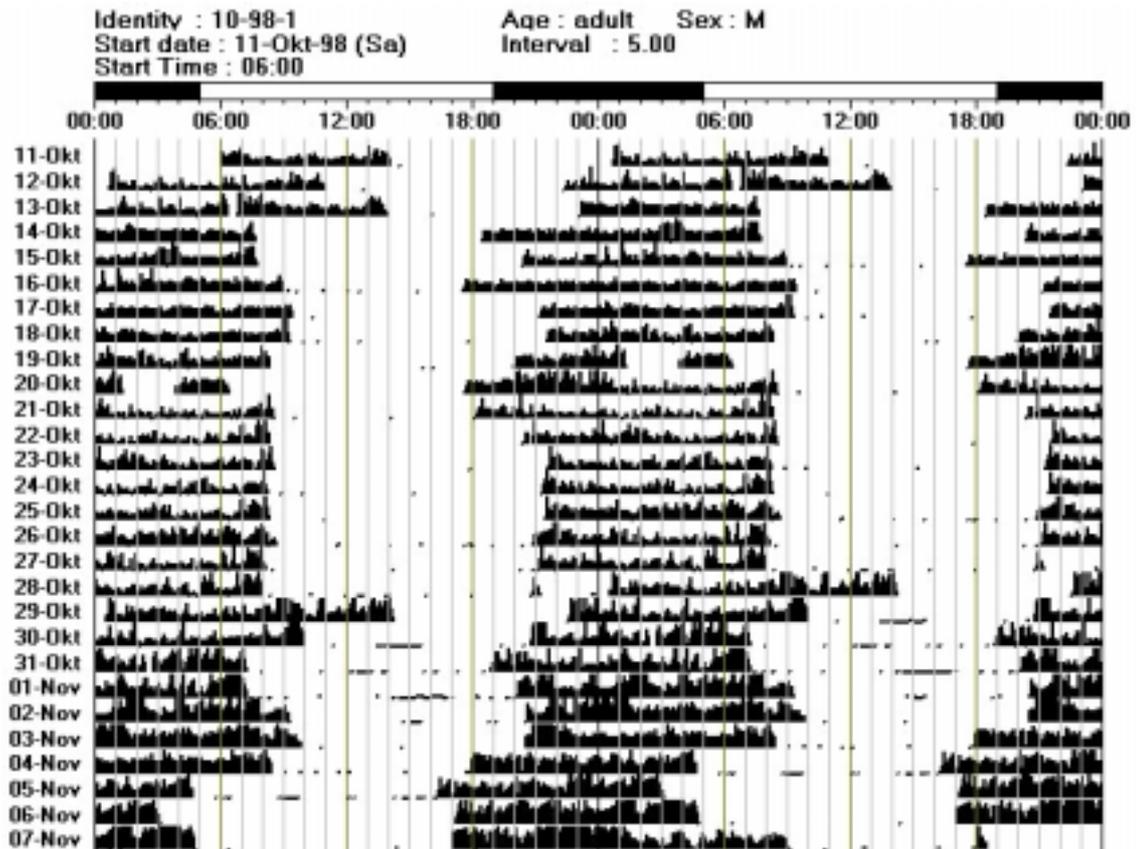
moderate – large patches of guard hairs missing. Usually noticeable on wet animal

heavy – pelage almost devoid of guard hairs. Always noticeable on wet animal

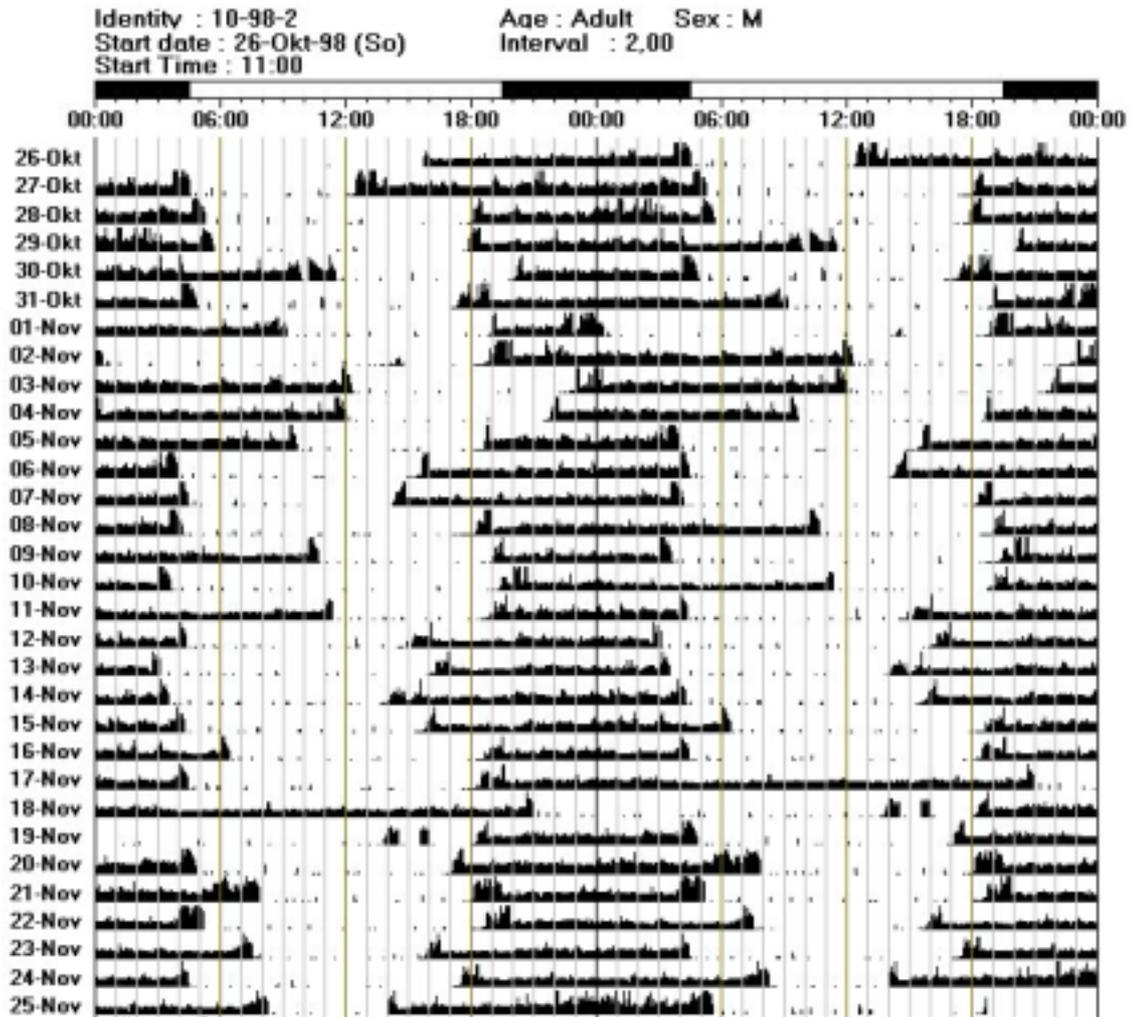
Temperature Charts:

Temperature charts show water (blue line), air (red line) and TDR-temperatures (black line, derived from time-depth recorder on the back of the platypus) over the logger-deployment time, respectively.

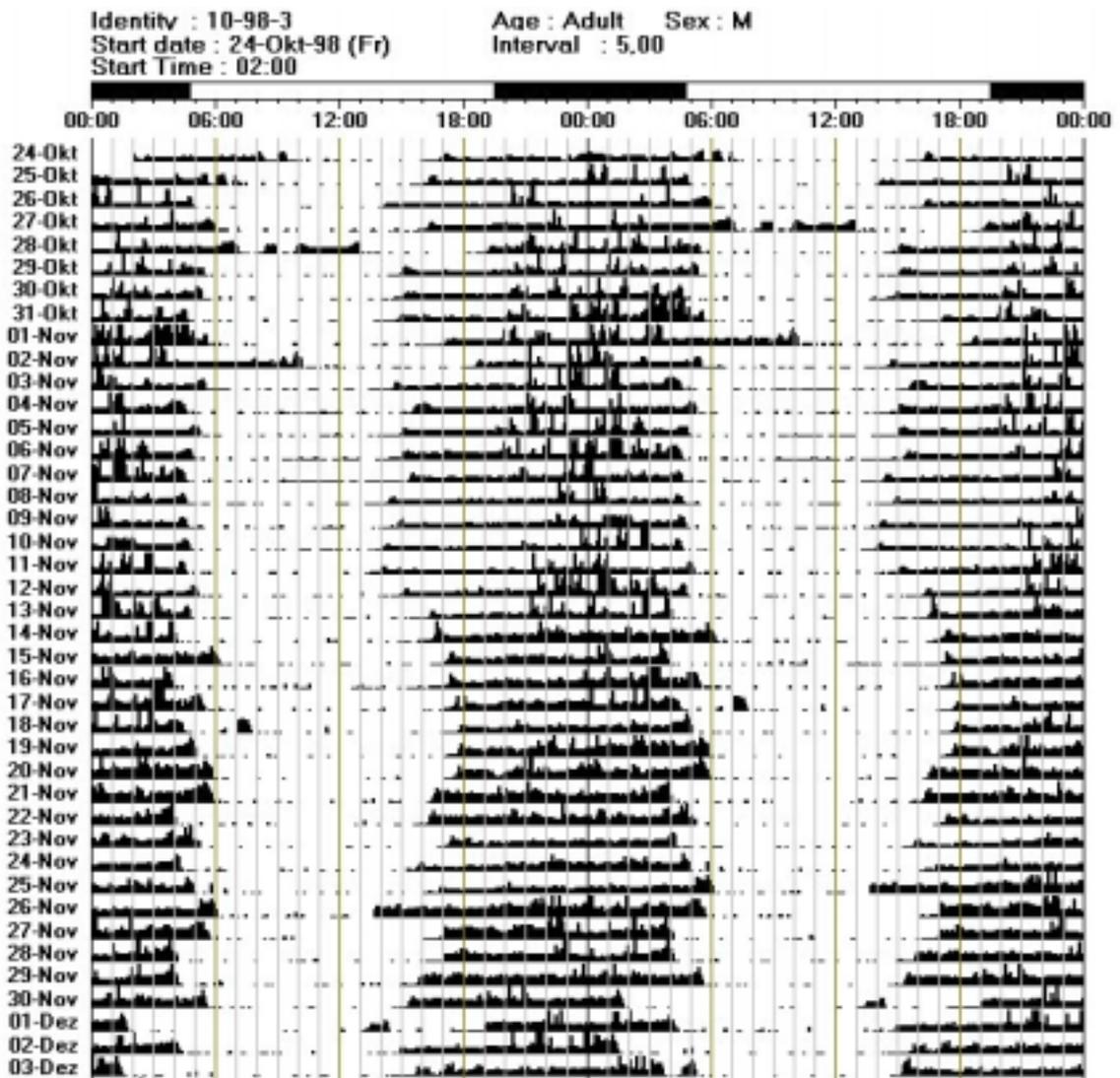
Identity:	10-98-1, Male, adult , Tag-No. 01C6-246B, transient
Season	Spring
Activity pattern	Nocturnal, Period 24 h (p<0.0025)
Site Type	Creek (Jennifer Creek)
Details	1.50 kg, Tail fat: 3, Bill: 49/52/72 mm, Body Length: 52 cm, Spur Class: E, Moulting class: light
Data logger	activity logger, AW 530048
Repeat	no



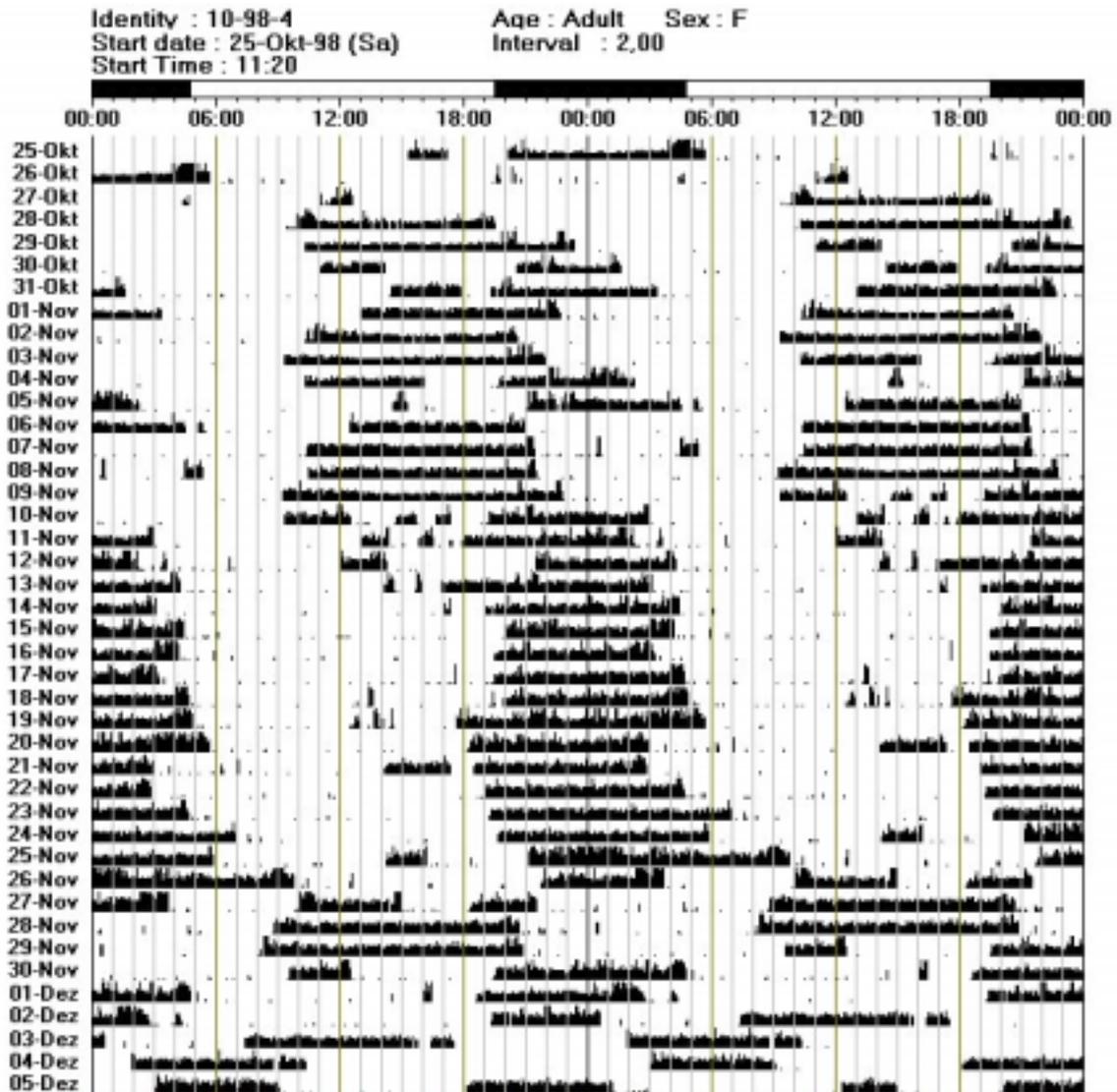
Identity:	10-98-2, Male, adult , Tag-No. 01D2-D5DC, resident
Season	Spring
Activity pattern	Mixed, Period 23.9 h (p<0.0061)
Site Type	Creek (Bare Mount Creek)
Details	1.82 kg, Tail fat: 2, Bill: 49/55/78 mm, Body Length: 55.5 cm, Spur Class: E, Moulting class: light
Data logger	activity logger, AW 511687
Repeat	no



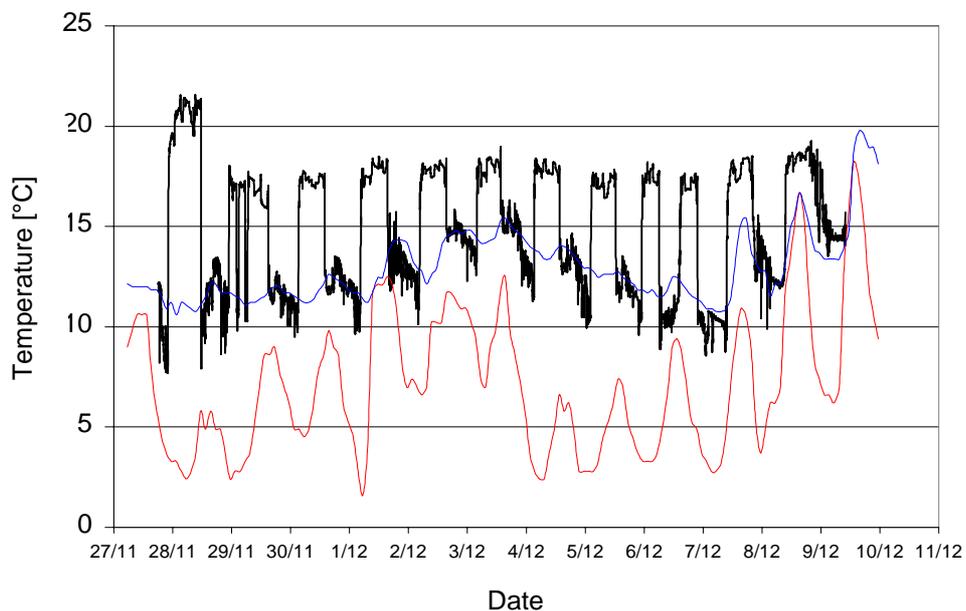
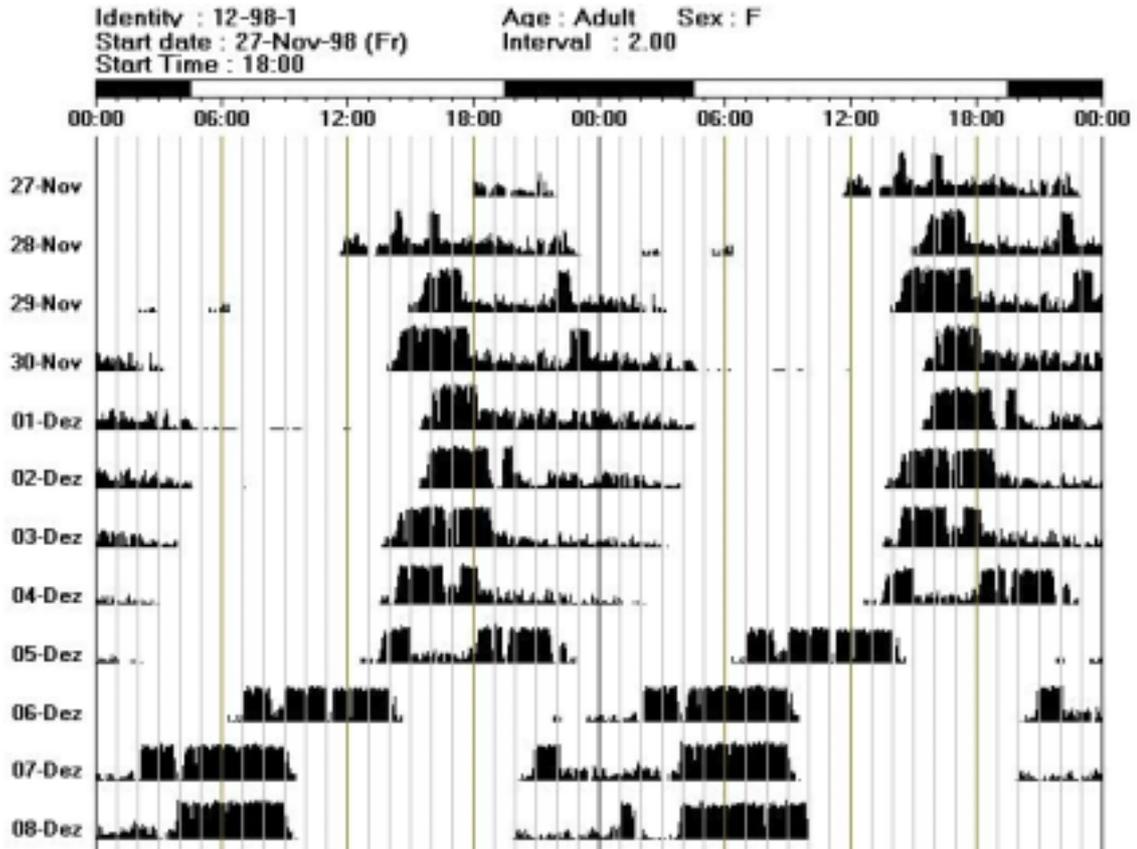
Identity:	10-98-3, Male, adult , Tag-No. 01D3-2F7F, transient
Season	Spring
Activity pattern	Nocturnal, Period 23.9 h ($p < 0.0025$)
Site Type	Creek (Bonds Creek)
Details	2.08 kg, Tail fat: 2, Bill: 49/53/78 mm, Body Length: 58 cm, Spur Class: F, Molt class: very light
Data logger	activity logger, AW 530048
Repeat	no



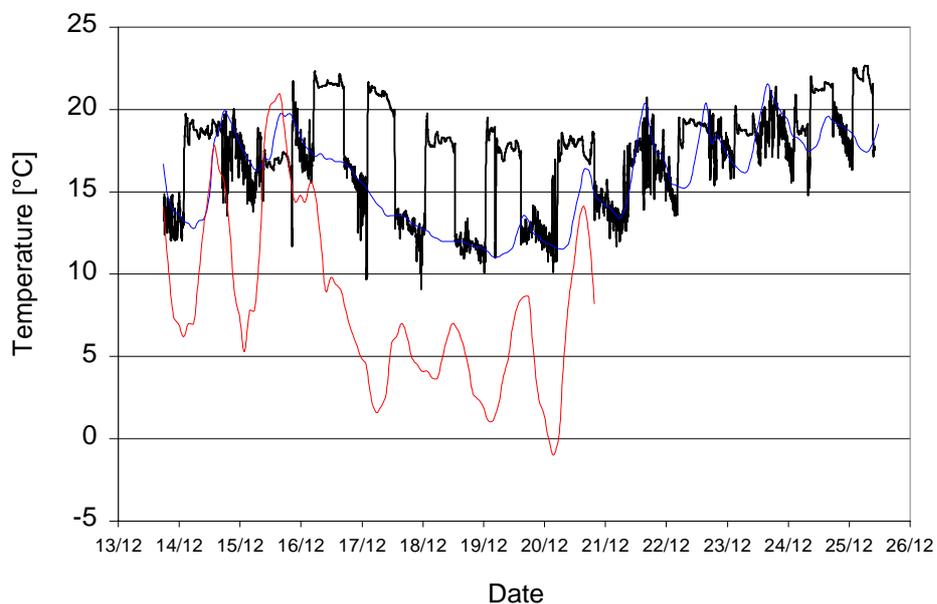
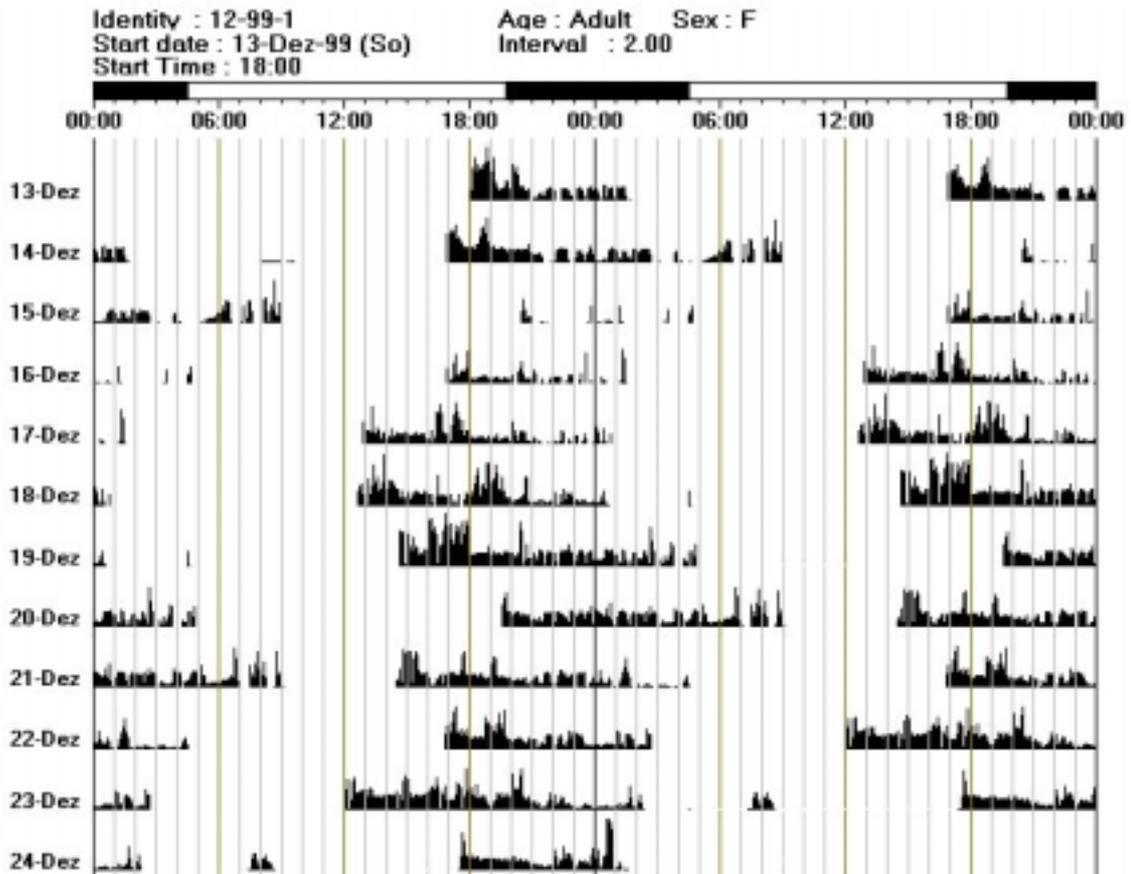
Identity:	10-98-4, Female, adult , Tag-No. 01C6-38D5, resident
Season	Spring
Activity pattern	Mixed, Period 24 h ($p < 0.0061$)
Site Type	Creek (Bonds Creek → Vale)
Details	1.47 kg, Tail fat: 2, Bill: 46/57/73 mm, Body Length: 50 cm, Spur Class: 0, Moulting class: light
Data logger	activity logger, AW 511914
Repeat	no



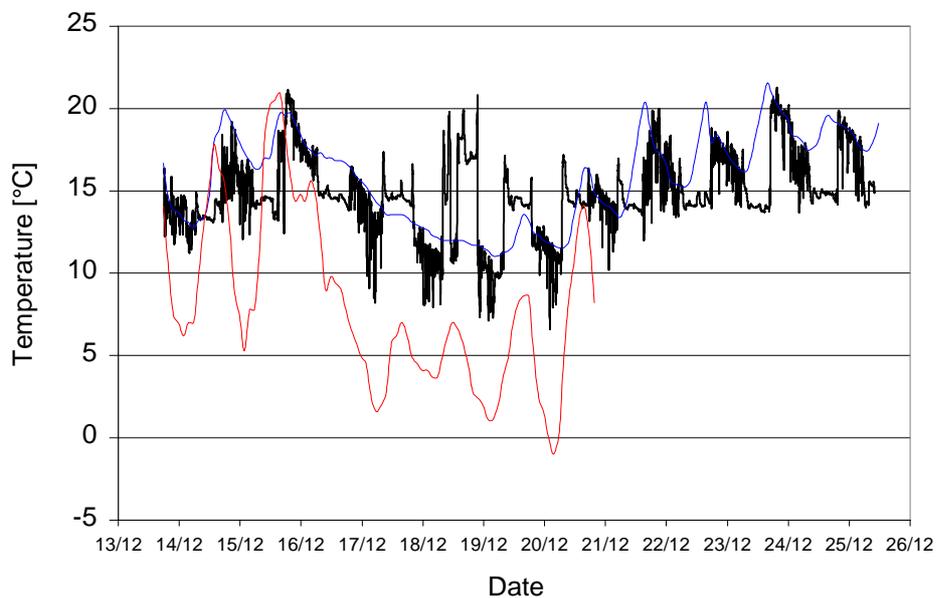
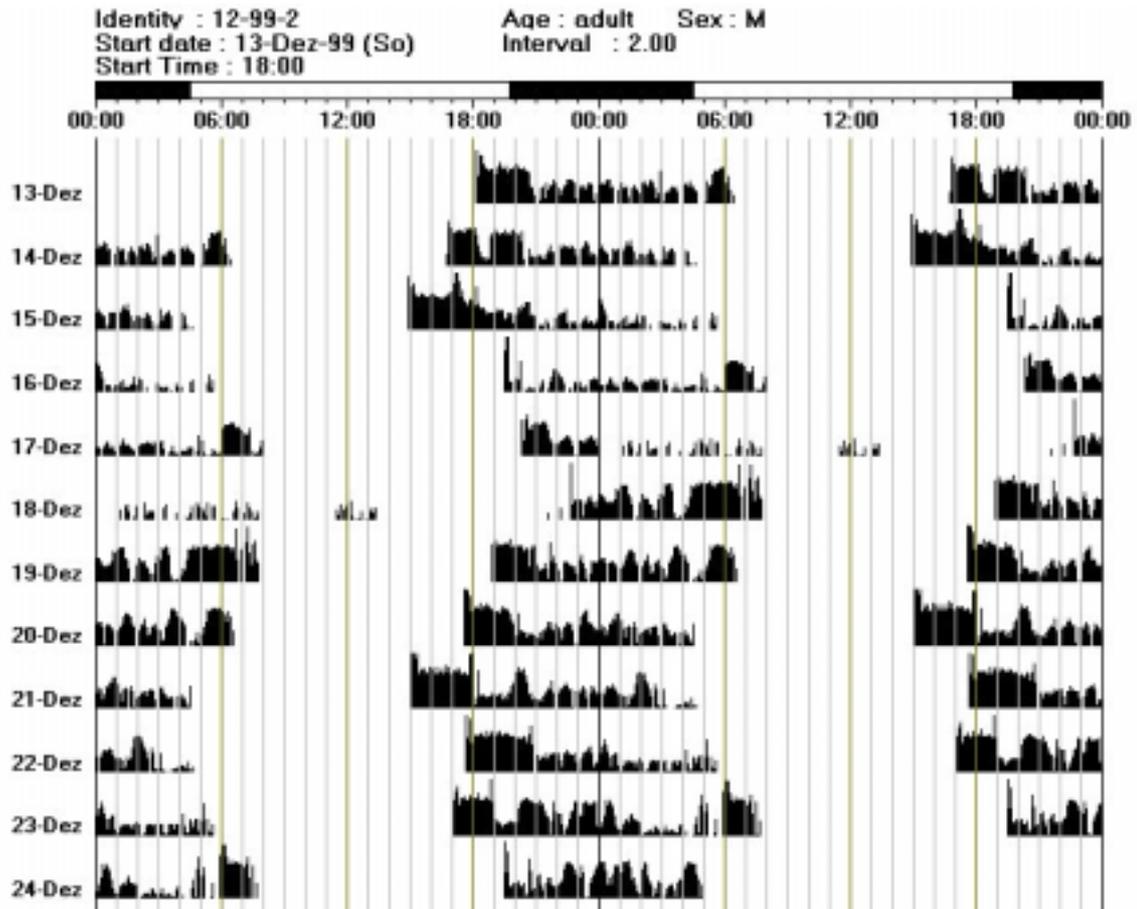
Identity:	12-98-1, Female, adult, Tag-No. 0075-F749, resident
Season	Summer
Activity pattern	Mixed – moon, Period 24.1 h (p<0.0061)
Site Type	Creek (Bare Mount Creek → Lea River)
Details	1.56 kg, Tail fat: 2, Bill: 46/52/72 mm, Body Length: 51 cm, Spur Class: 0, Moulting Class: very light
Data logger	time-depth recorder, TDR 1995
Repeat	yes, 03-98-5 (AL)



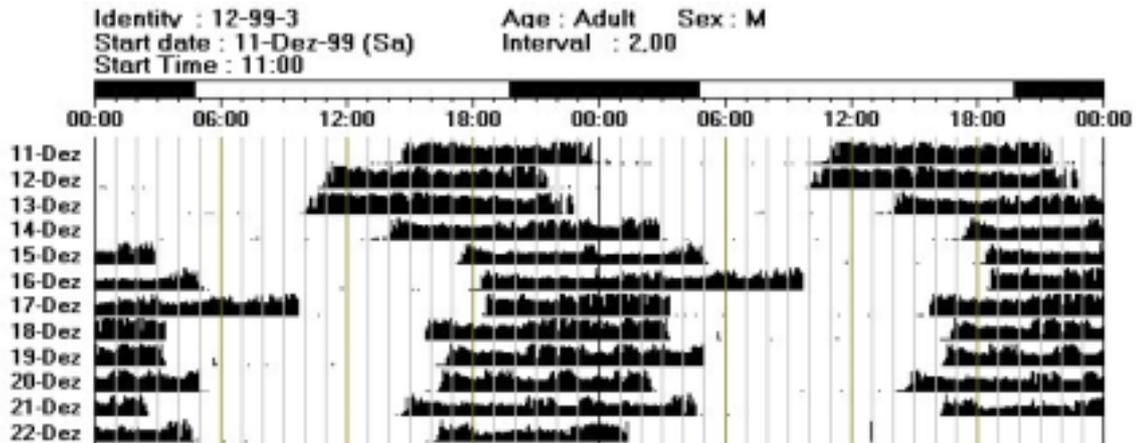
Identity:	12-99-1, Female, adult, Tag-No. 00F6-438A, resident
Season	Summer
Activity pattern	Nocturnal, Period 24 h (p<0.0061)
Site Type	Mixed (Bare Mount Creek → Deep Hole)
Details	1.55 kg, Tail fat: 2, Bill: 44/54/73 mm, Body Length: 48.5 cm, Spur Class: 0, Moulting Class: light
Data logger	time-depth recorder, TDR 2282
Repeat	yes, 06-99-3 (AL)



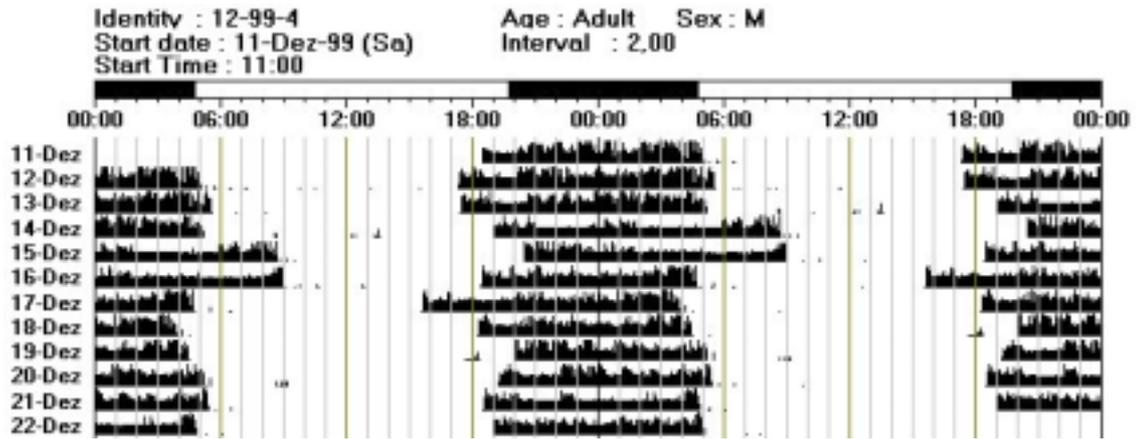
Identity:	12-99-2, Male, adult, Tag-No. 0077-C753, resident
Season	Summer
Activity pattern	Nocturnal, Period 24 h ($p < 0.0061$)
Site Type	Lake (Deep Hole)
Details	2.06 kg, Tail fat: 3, Bill: 51/59/80 mm, Body Length: 60 cm, Spur Class: E, Moul Class: light
Data logger	time-depth recorder, TDR 2268
Repeat	no



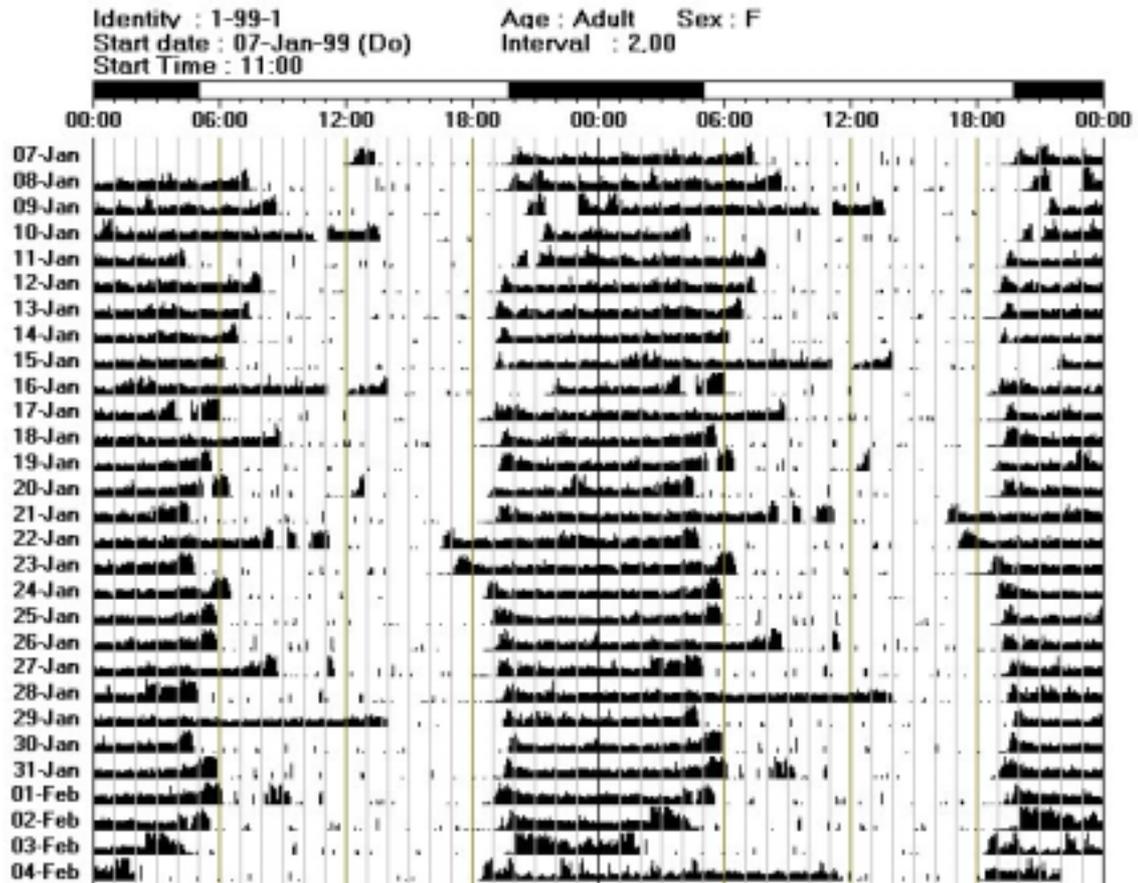
Identity:	12-99-3, Male, adult , Tag-No. 01C5-OEAB, resident
Season	Summer
Activity pattern	Mixed – moon?, Period 24.5 h (p<0.0061)
Site Type	Lake (Deep Hole)
Details	1.97 kg, Tail fat: 3, Bill: 48/56/77 mm, Body Length: 57 cm, Spur Class: E, Moulting class: light
Data logger	activity logger, AW 511687
Repeat	no



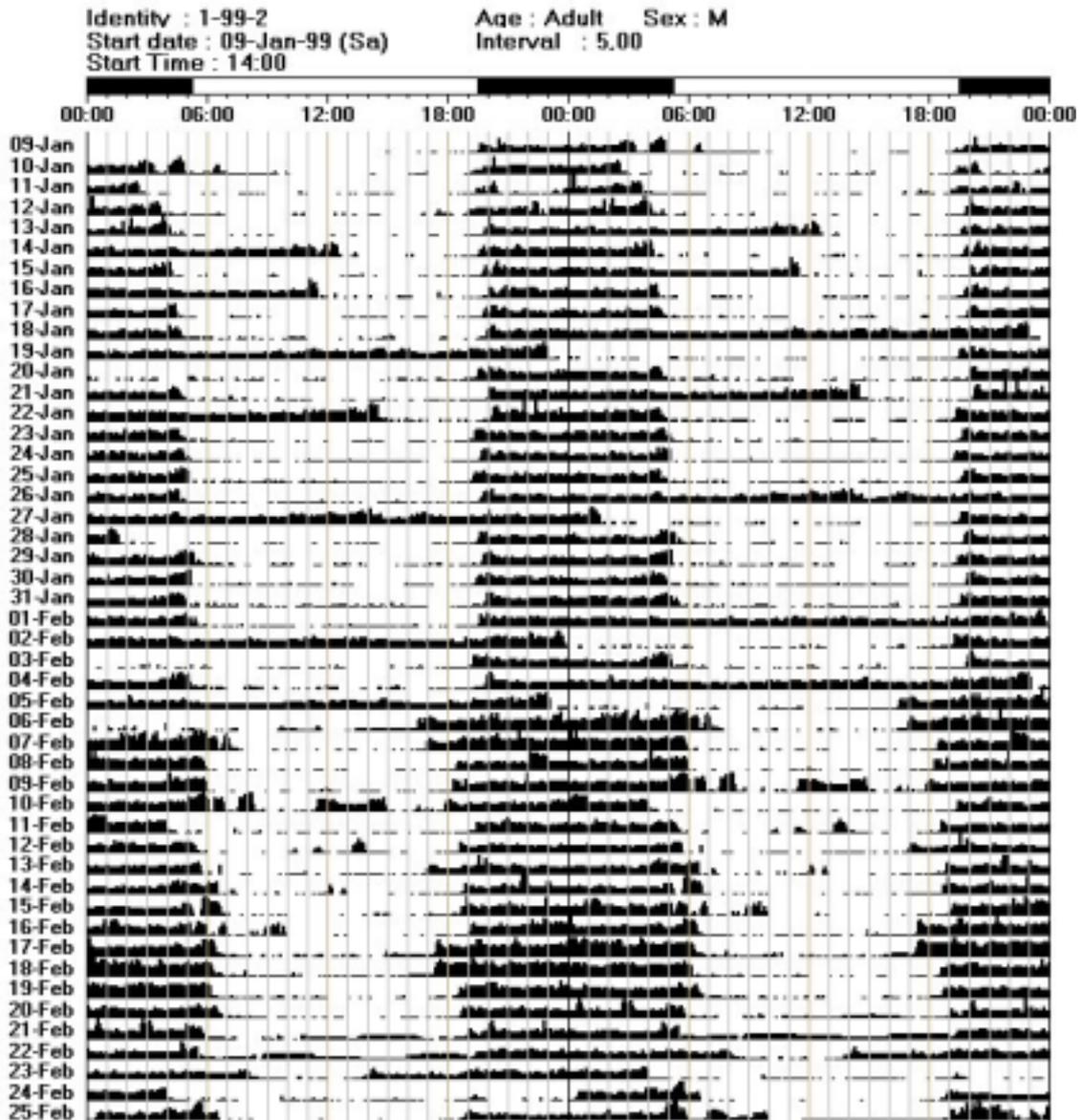
Identity:	12-99-4, Male, adult , Tag-No. 01F7-E8A9, resident
Season	Summer
Activity pattern	Nocturnal, Period 24 h (p<0.0061)
Site Type	Mixed (Bare Mount Creek → Platypus Playground)
Details	1.72 kg, Tail fat: 3, Bill: 48/55/75 mm, Body Length: 55 cm, Spur Class: E, Molt class: moderate
Data logger	activity logger, AW 511914
Repeat	no



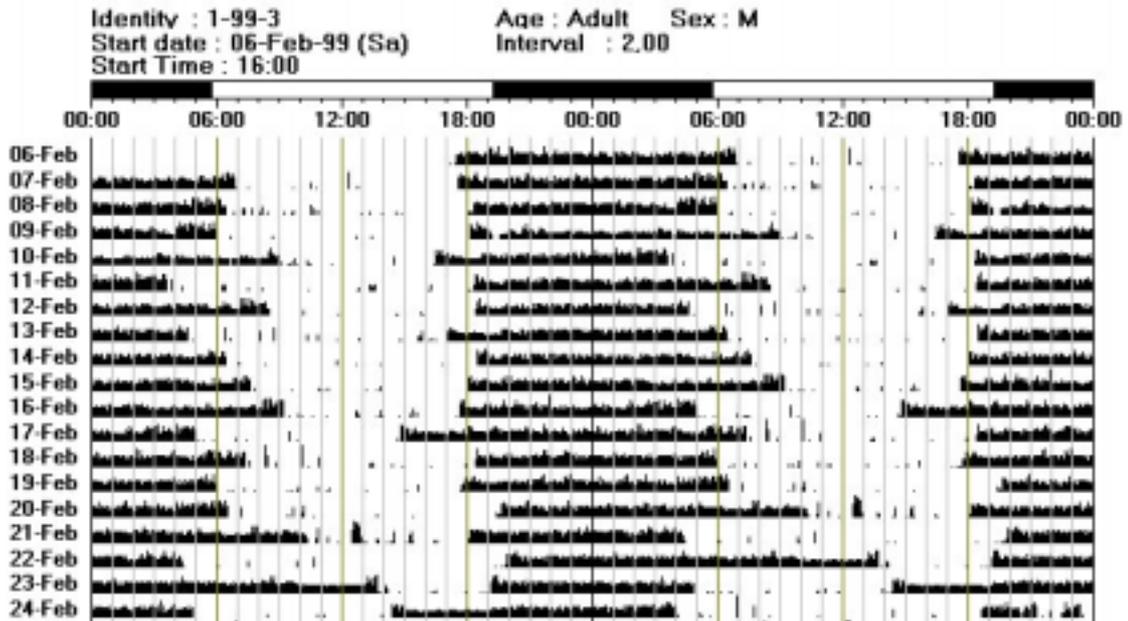
Identity:	01-99-1, Female, adult, Tag-No. 0064-3898, resident
Season	Summer
Activity pattern	Nocturnal, Period 23.9 h ($p < 0.0061$)
Site Type	Creek (Bare Mount Creek)
Details	1.42 kg, Tail fat: 2, Bill: 45/50/65 mm, Body Length: 52 cm, Spur Class: 0, Moulting Class: light
Data logger	activity logger, AW 511687
Repeat	yes, 2-98-4 (AL)



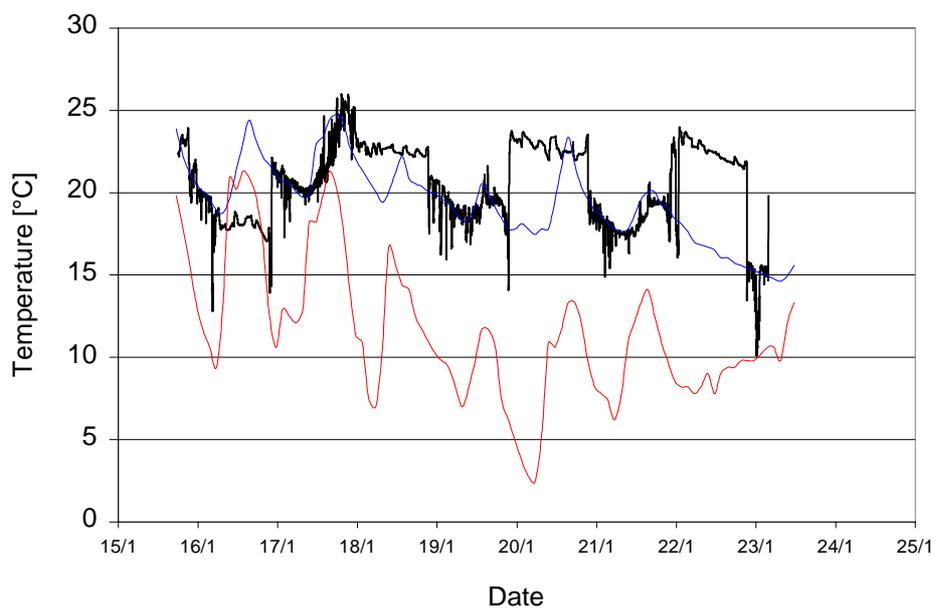
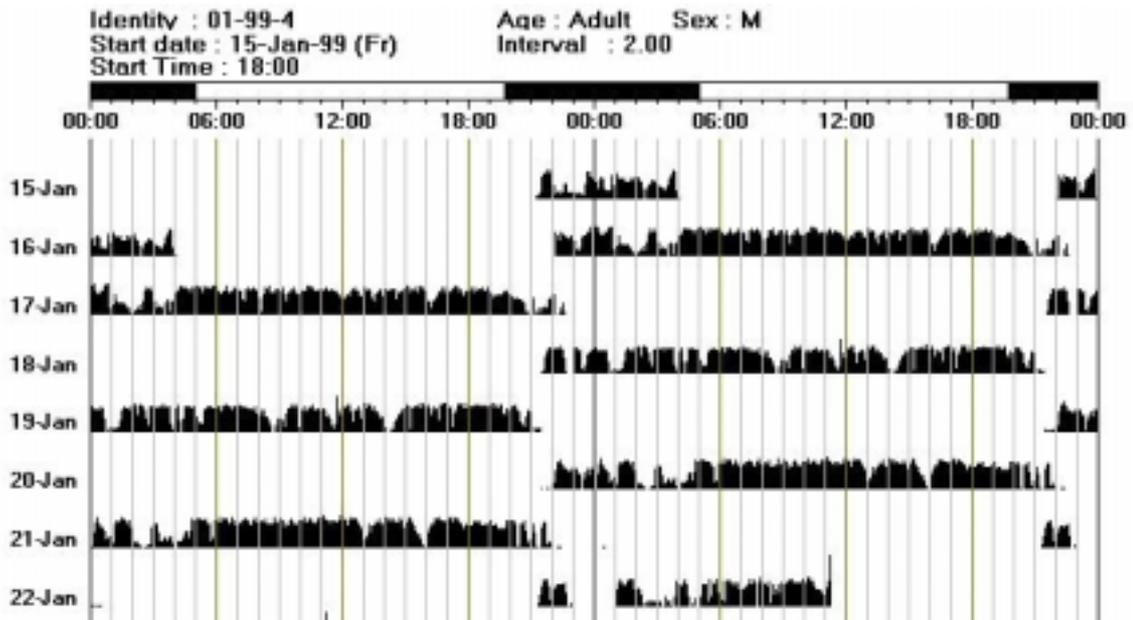
Identity:	01-99-2, Male, adult, Tag-No. 0124-E365, transient
Season	Summer
Activity pattern	Mixed – mainly nocturnal, Period 24 h ($p < 0.0025$)
Site Type	Creek (Bonds Creek → DLW Creek)
Details	2.19 kg, Tail fat: 2, Bill: 52/59/81 mm, Body Length: 56 cm, Spur Class: E, Moulting Class: moderate
Data logger	activity logger, AW 530048
Repeat	no



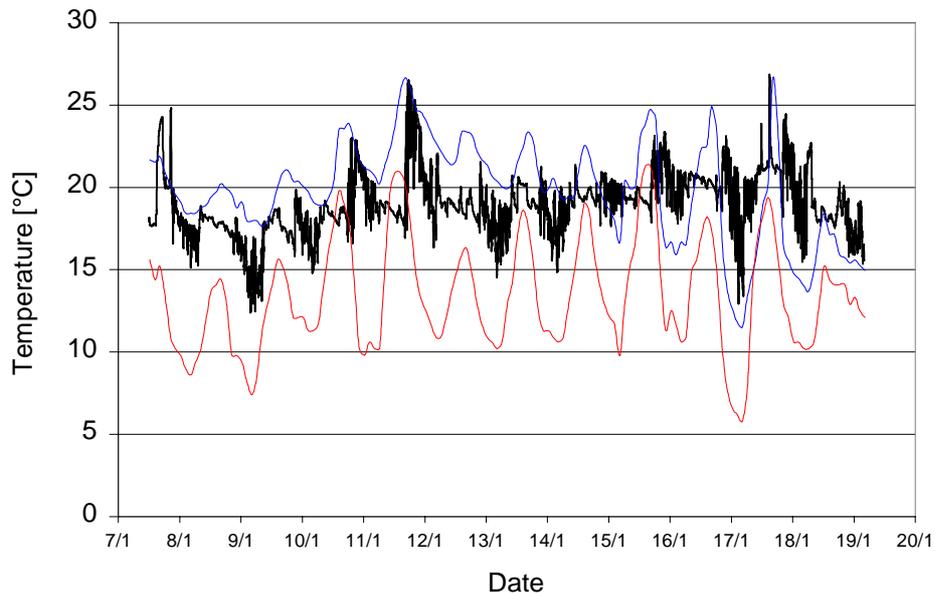
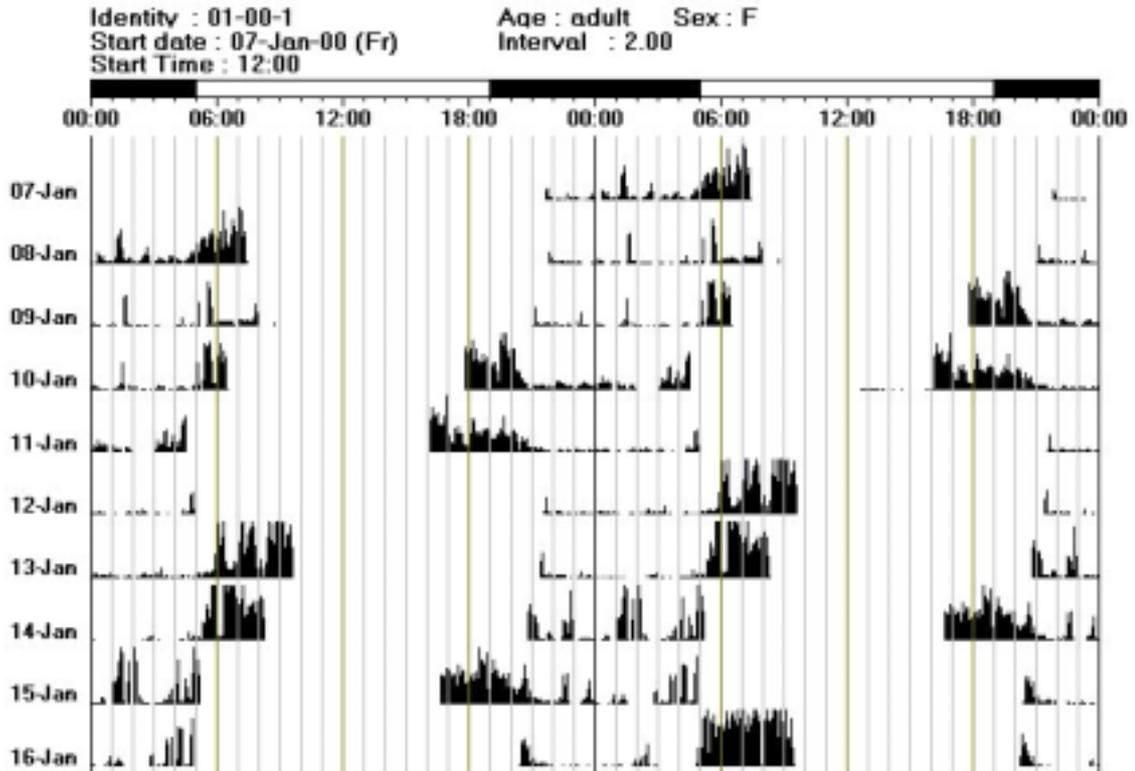
Identity:	01-99-3, Male, adult, Tag-No. 01C6-D017, transient
Season	Summer
Activity pattern	Nocturnal, Period 24.1 h ($p < 0.0061$)
Site Type	Mixed (Deep Hole → Lea River)
Details	2.24 kg, Tail fat: 2, Bill: 51/59/82 mm, Body Length: 57.5 cm, Spur Class: E, Moulting Class: moderate
Data logger	activity logger, AW 511914
Repeat	no



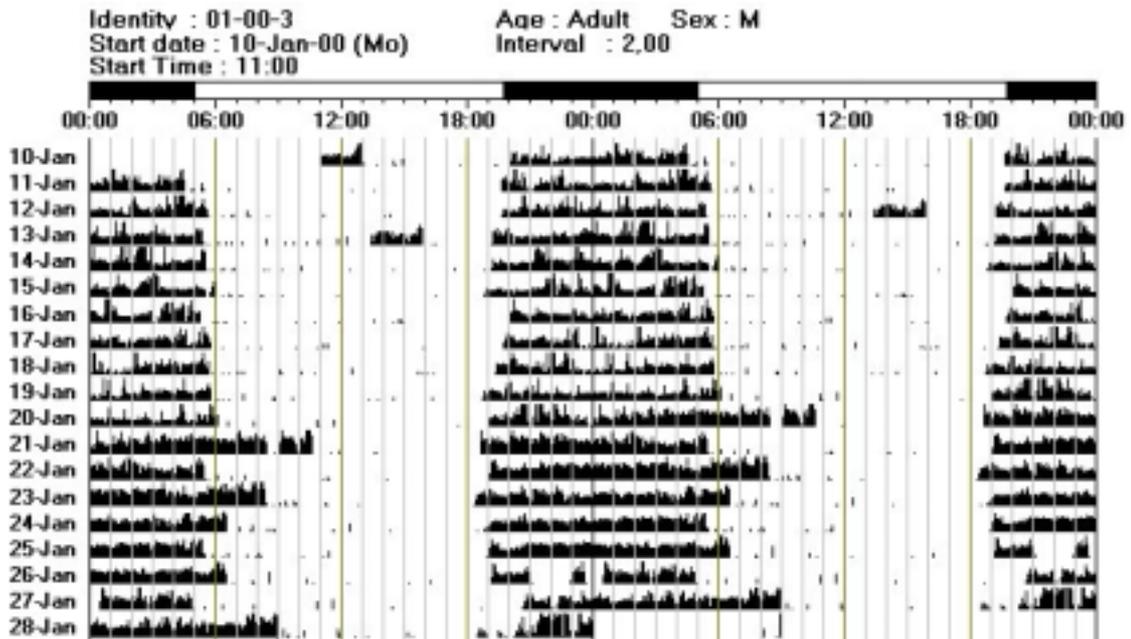
Identity:	01-99-4, Male, adult, Tag-No. 0064-2E8F, resident
Season	Summer
Activity pattern	Mixed, Period 48 h
Site Type	Lake (Platypus Playground)
Details	2.27 kg, Tail fat: 2, Bill: 52/59/83 mm, Body Length: 60 cm, Spur Class: E, Moul Class: light
Data logger	time-depth recorder, TDR 1995
Repeat	no



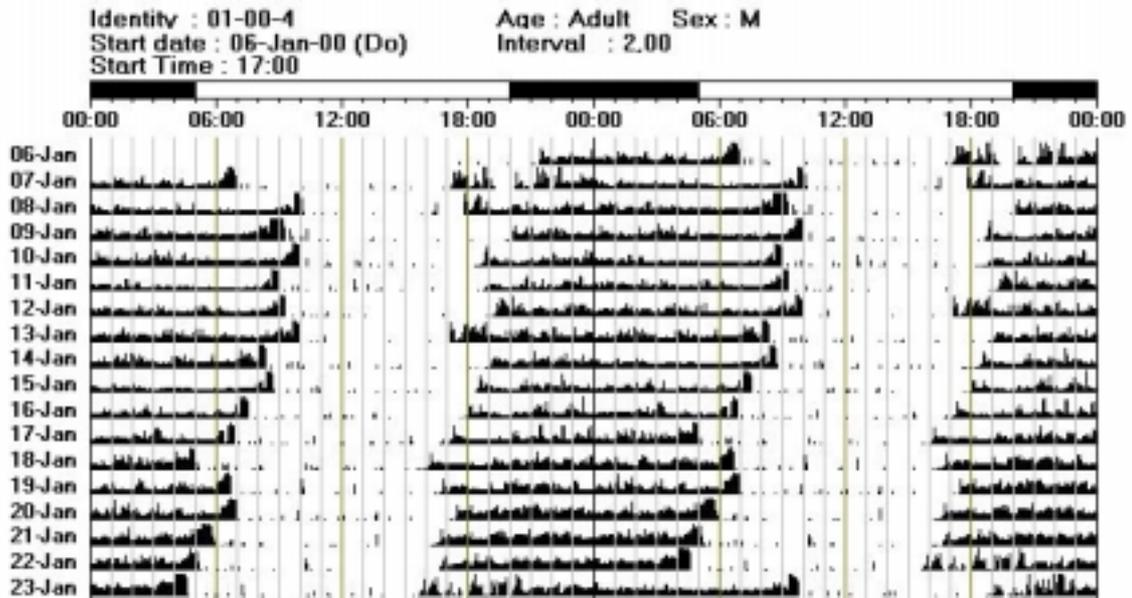
Identity:	01-00-1, Female, adult, Tag-No. 0075-F17E, resident
Season	Summer
Activity pattern	Nocturnal, Period 24 h (p<0.0061)
Site Type	Lake (Deep Hole)
Details	1.45 kg, Tail fat: 3, Bill: 44/55/72 mm, Body Length: 53 cm, Spur Class: 0, Moulting Class: moderate
Data logger	time-depth recorder, TDR 2282
Repeat	yes, 04-98-3 (AL)



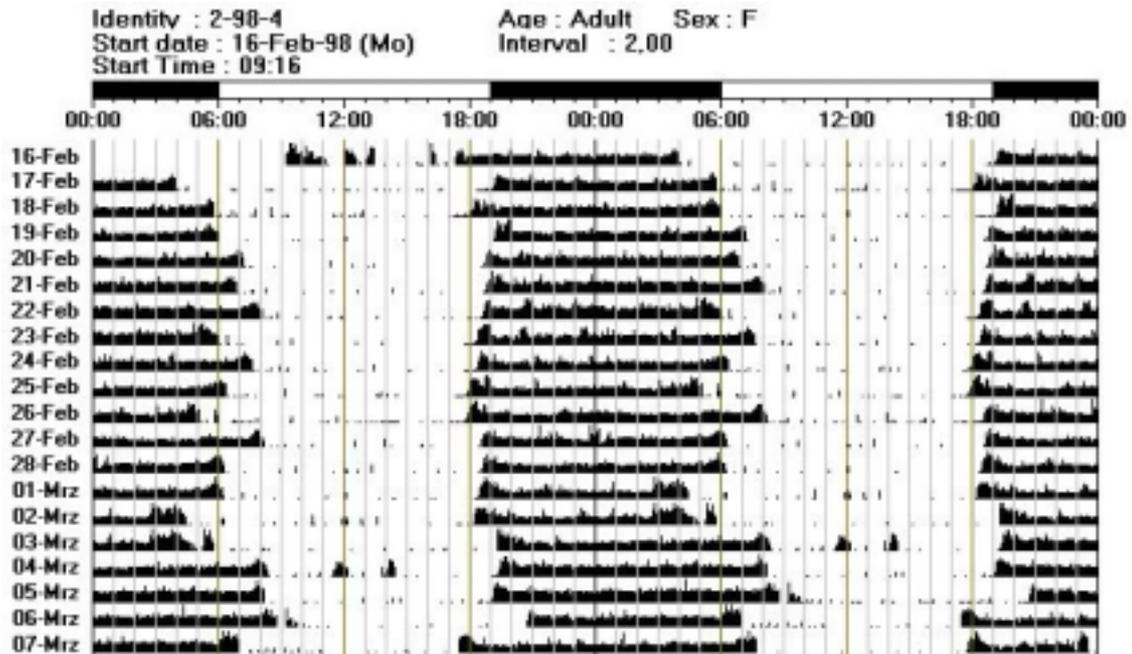
Identity:	01-00-3, Male, adult, Tag-No. 01D0-CCAD, resident
Season	Summer
Activity pattern	Nocturnal, Period 24 h (p<0.0061)
Site Type	Mixed (Platypus Playground → Jennifer Creek)
Details	1.73 kg, Tail fat: 3, Bill: 47/55/75 mm, Body Length: 54 cm, Spur Class: E, Molt Class: very light
Data logger	activity logger, AW 511687
Repeat	yes, 07-99-2 (TDR)



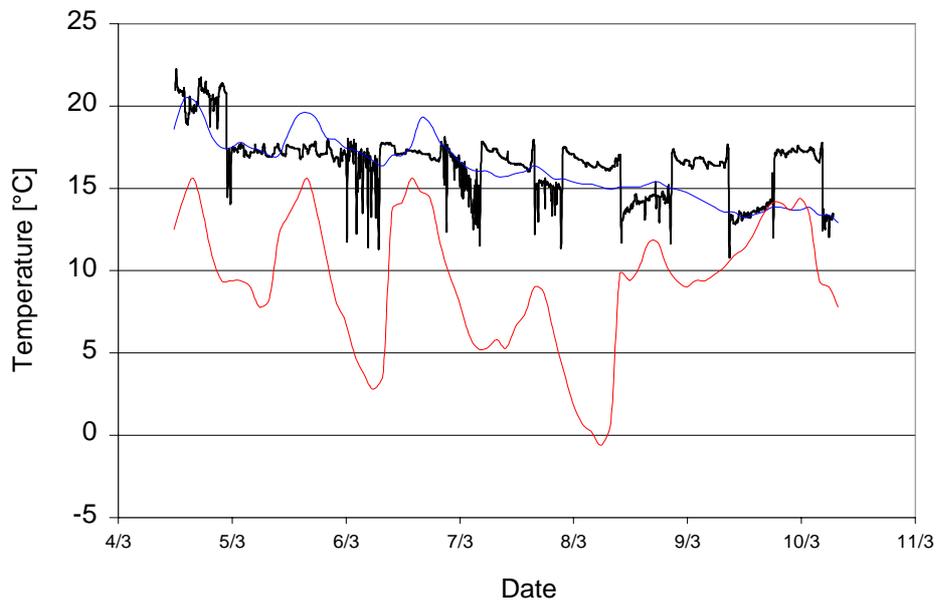
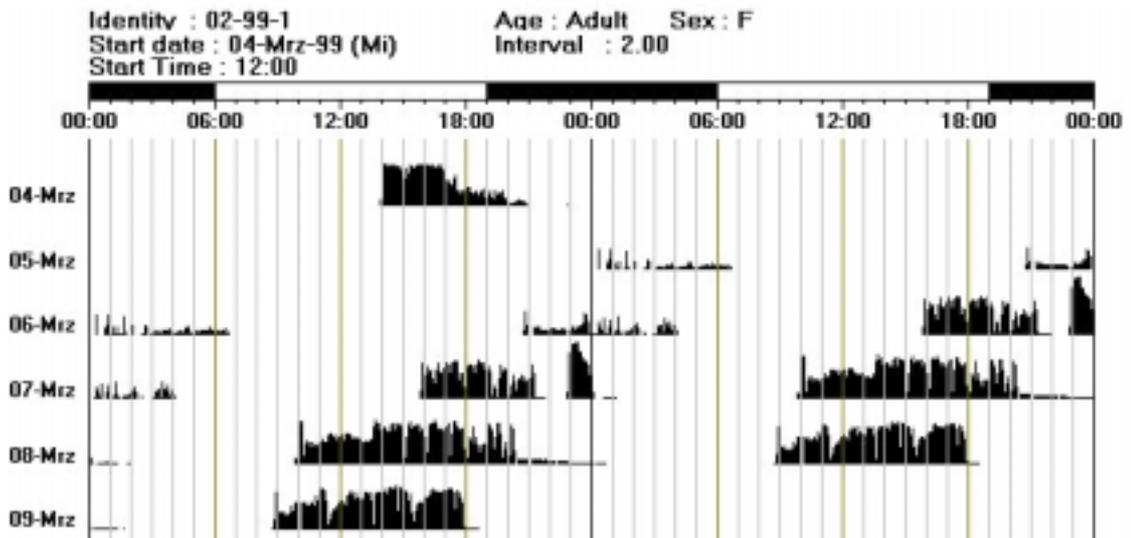
Identity:	01-00-4, Male, adult, Tag-No. 01C6-6FE2, resident
Season	Summer
Activity pattern	Nocturnal, Period 23.7 h ($p < 0.0061$)
Site Type	Lake (Deep Hole)
Details	2.46 kg, Tail fat: 3, Bill: 52/59/77 mm, Body Length: 61 cm, Spur Class: E, Molt Class: light
Data logger	activity logger, AW 530048
Repeat	no



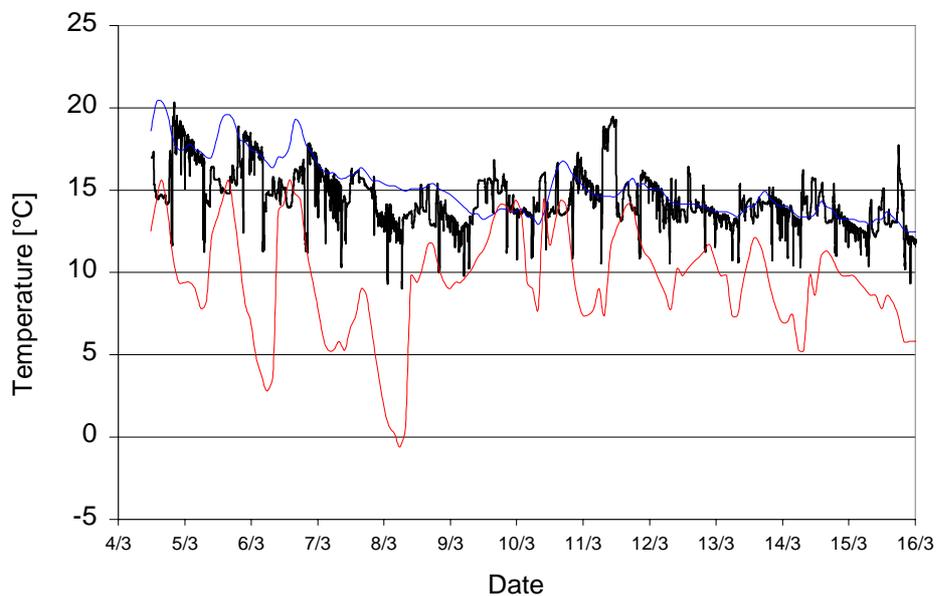
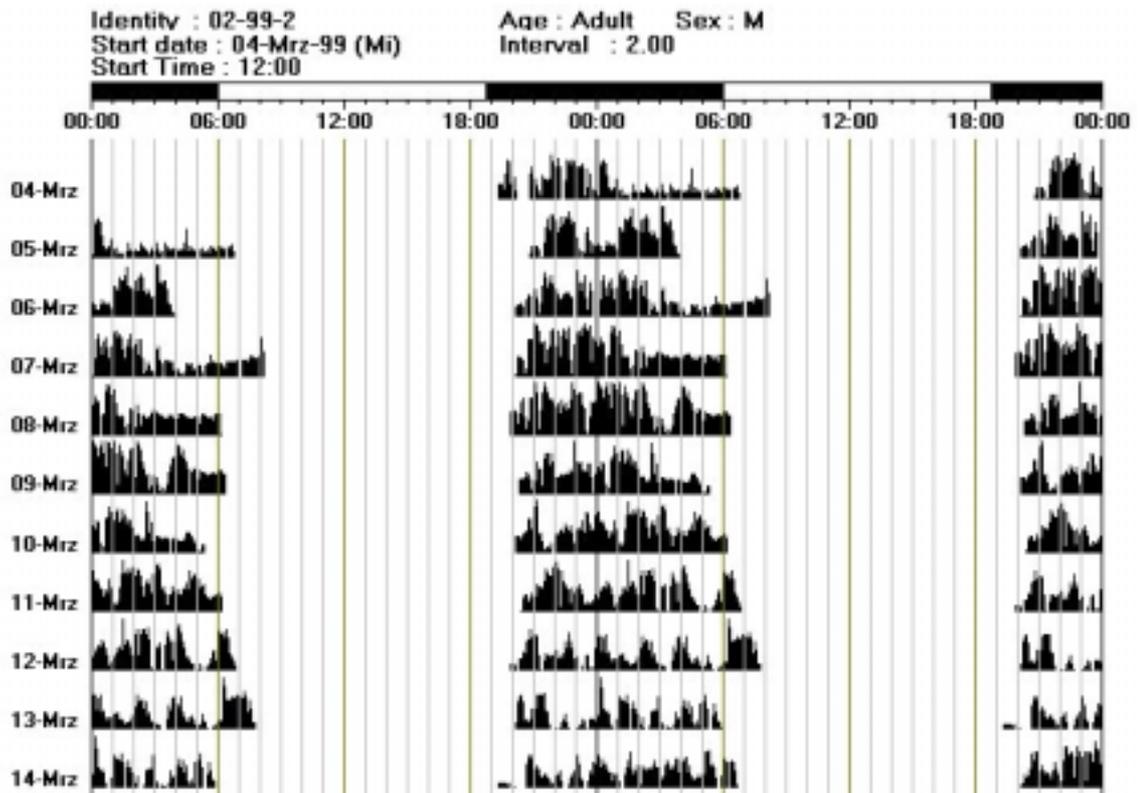
Identity:	02-98-4, Female, adult, Tag-No. 0064-3898, resident
Season	Summer/Autumn
Activity pattern	Nocturnal, Period 24 h (p<0.0061)
Site Type	Creek (Bare Mount Creek)
Details	1.39 kg, Tail fat: 3, Bill: 42/50/65 mm, Body Length: 49 cm, Spur Class: 0, Moulting Class: light
Data logger	activity logger, AW 530044
Repeat	yes, 01-99-1 (AL)



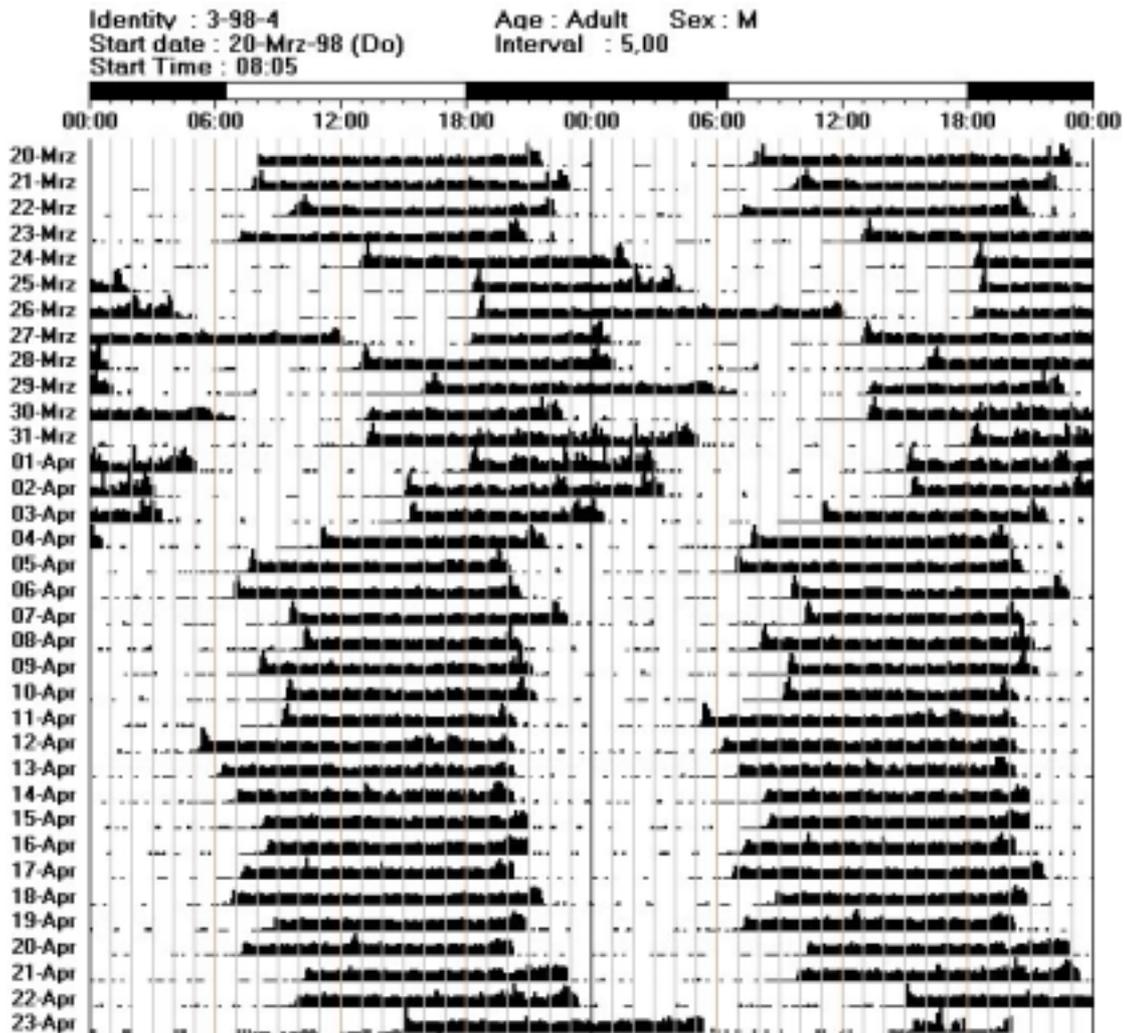
Identity:	02-99-1, Female, adult, Tag-No. 0075-F36D, resident
Season	Summer
Activity pattern	Mixed – moon?, Period not significant
Site Type	Mixed (Platypus Playground → Forest Rivulet)
Details	1.41 kg, Tail fat: 3, Bill: 43/54/72 mm, Body Length: 51 cm, Spur Class: 0, Moulting Class: very light
Data logger	time-depth recorder, TDR 1995
Repeat	no



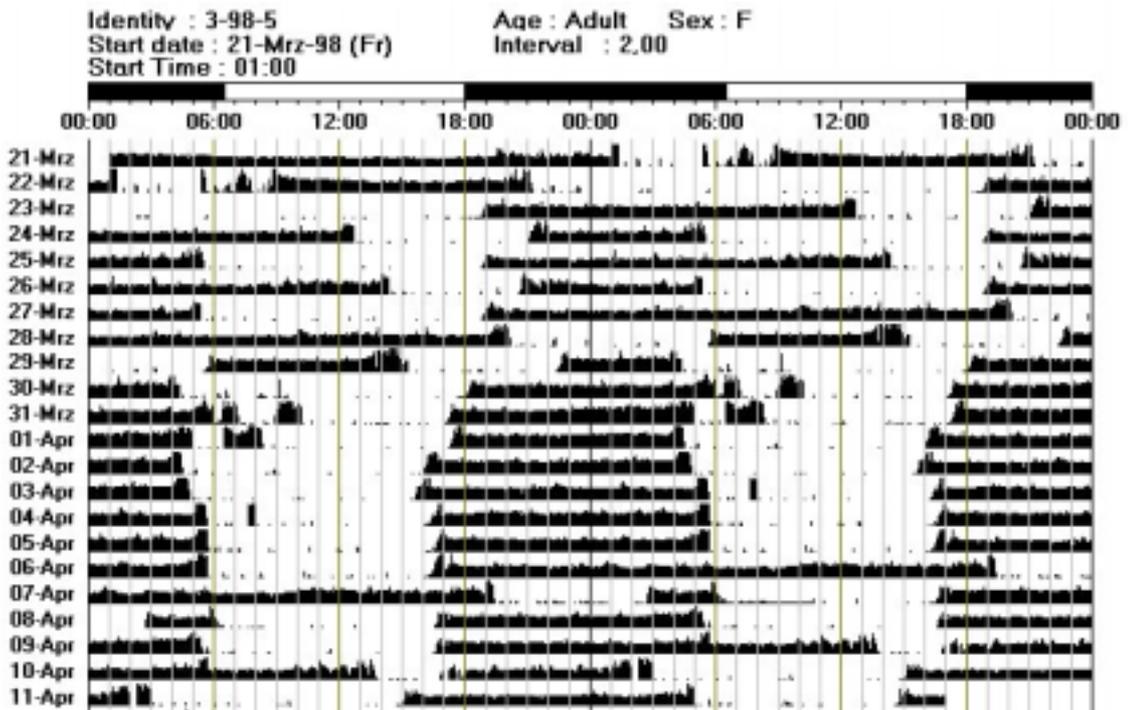
Identity:	02-99-2, Male, adult, Tag-No. 01F7-F0F0, resident
Season	Summer
Activity pattern	Nocturnal, Period 24 h ($p < 0.0061$)
Site Type	Lake (Platypus Playground)
Details	2.10 kg, Tail fat: 2, Bill: 49/57/77 mm, Body Length: 59 cm, Spur Class: E, Moulting Class: none
Data logger	time-depth recorder, TDR 2268
Repeat	no



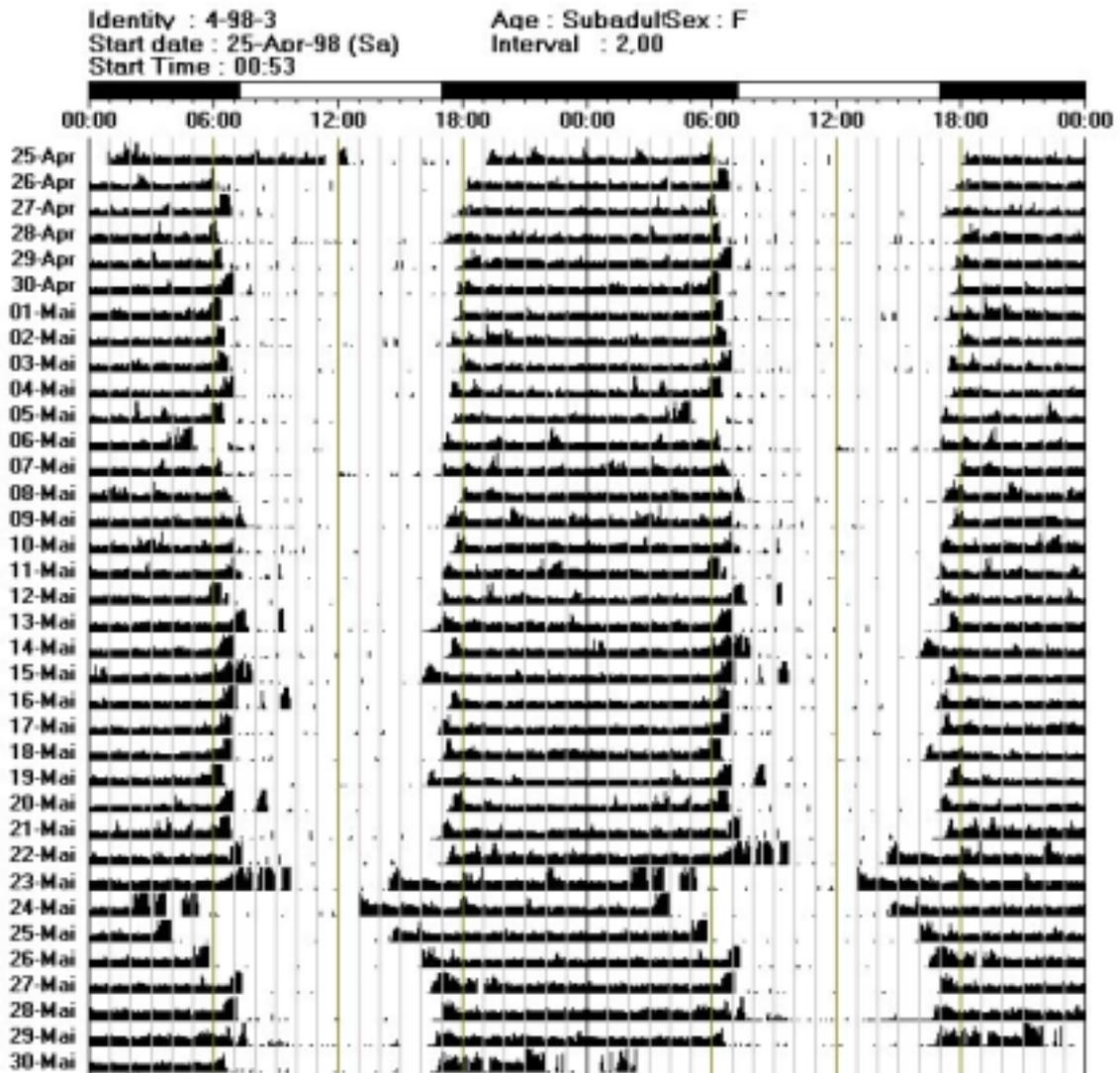
Identity:	03-98-4, Male, adult, Tag-No. 0064-6178, transient
Season	Autumn
Activity pattern	Mixed – moon, Period 23.9 h (p<0.0025)
Site Type	Creek (Bare Mount Creek)
Details	2.20 kg, Tail fat: 3, Bill: 52/62/83 mm, Body Length: 60 cm, Spur Class: E, Moulting Class: very light
Data logger	activity logger, AW 530048
Repeat	no



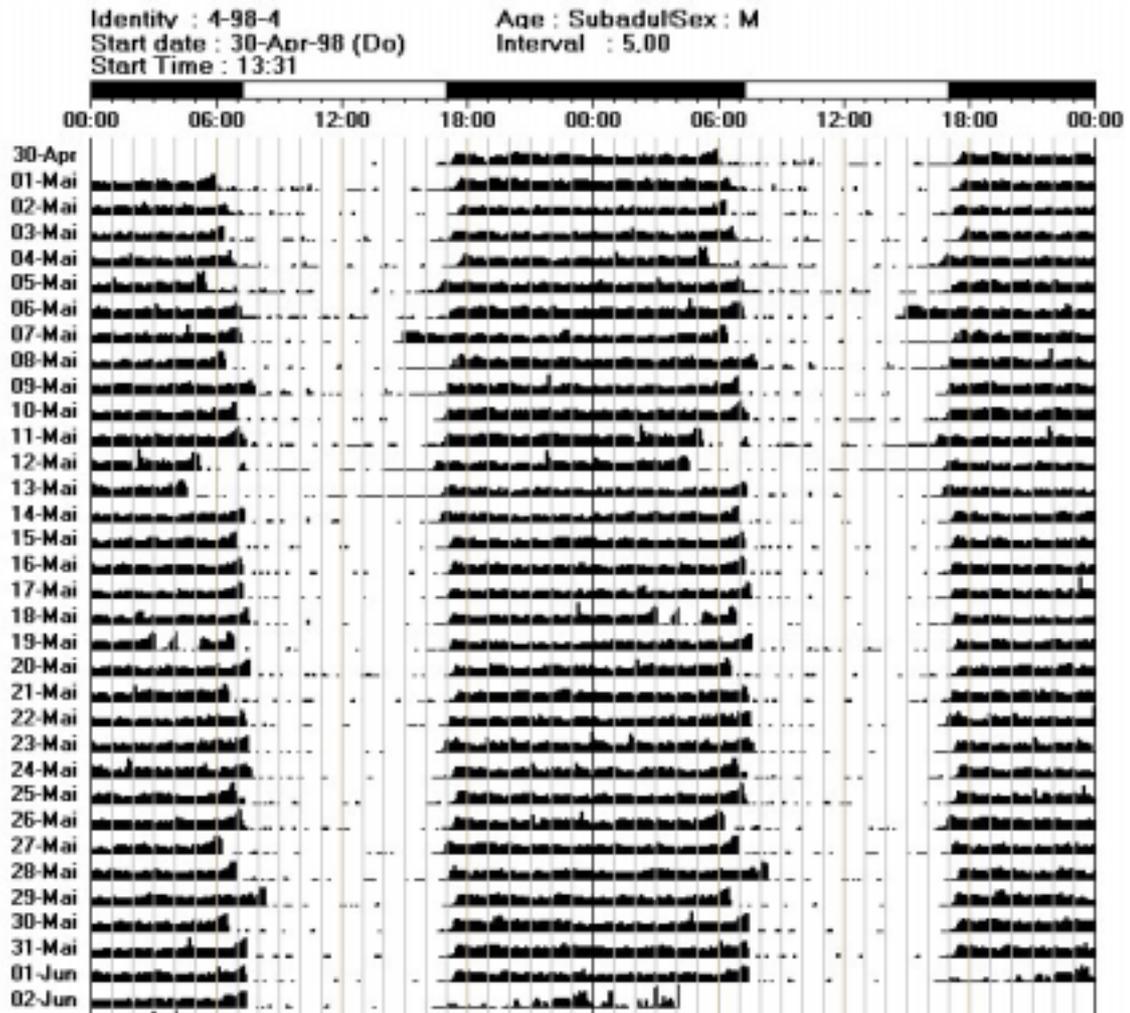
Identity:	03-98-5, Female, adult, Tag-No. 0075-F749, resident
Season	Autumn
Activity pattern	Mixed, Period 23.9 h (p<0.0061)
Site Type	Creek (Bare Mount Creek → Lea River)
Details	1.50 kg, Tail fat: 3, Bill: 46/52/70 mm, Body Length: 48 cm, Spur Class: 0, Moulting Class: none
Data logger	activity logger, AW 530044
Repeat	yes, 11-98-1 (TDR)



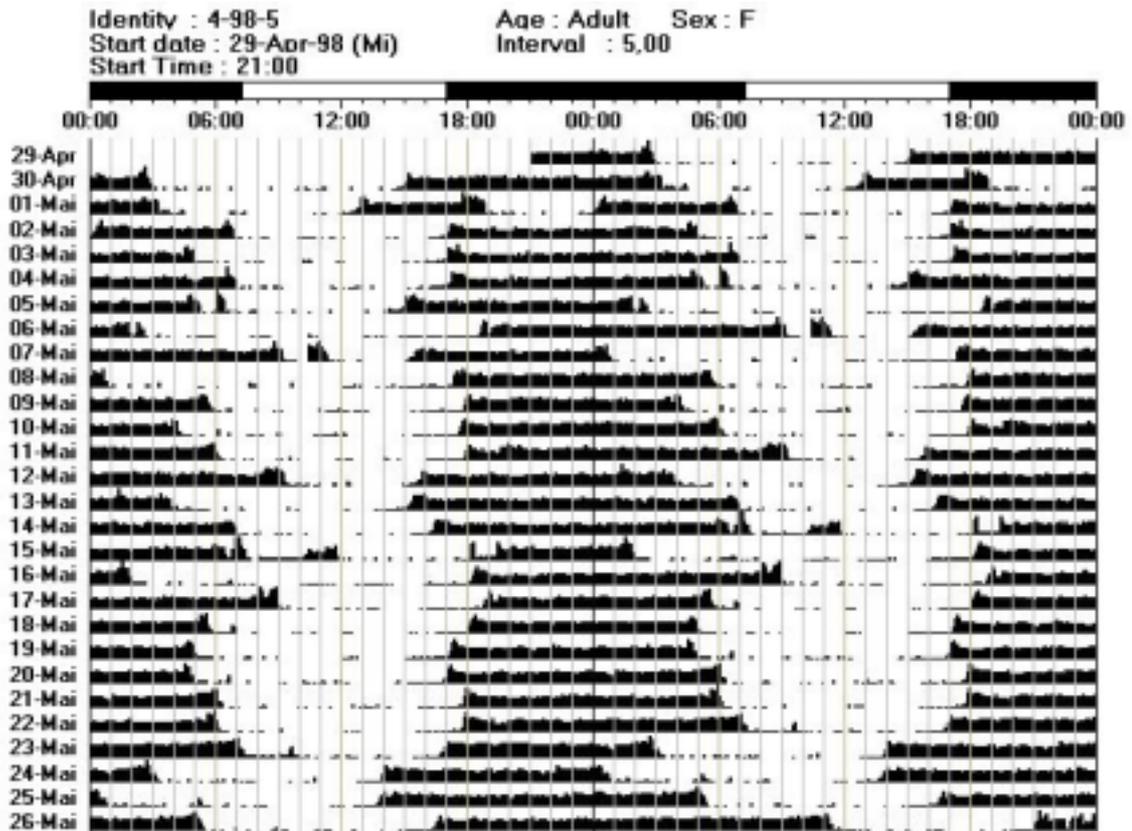
Identity:	04-98-3, Female, subadult, Tag-No. 0075-F17E, resident
Season	Autumn
Activity pattern	Nocturnal, Period 24 h (p<0.0061)
Site Type	Lake (Deep Hole)
Details	1.22 kg, Tail fat: 3, Bill: 45/53/71 mm, Body Length: 48 cm, Spur Class: 0, Moul Class: light
Data logger	activity logger, AW 511438
Repeat	yes, 01-00-1 (TDR)



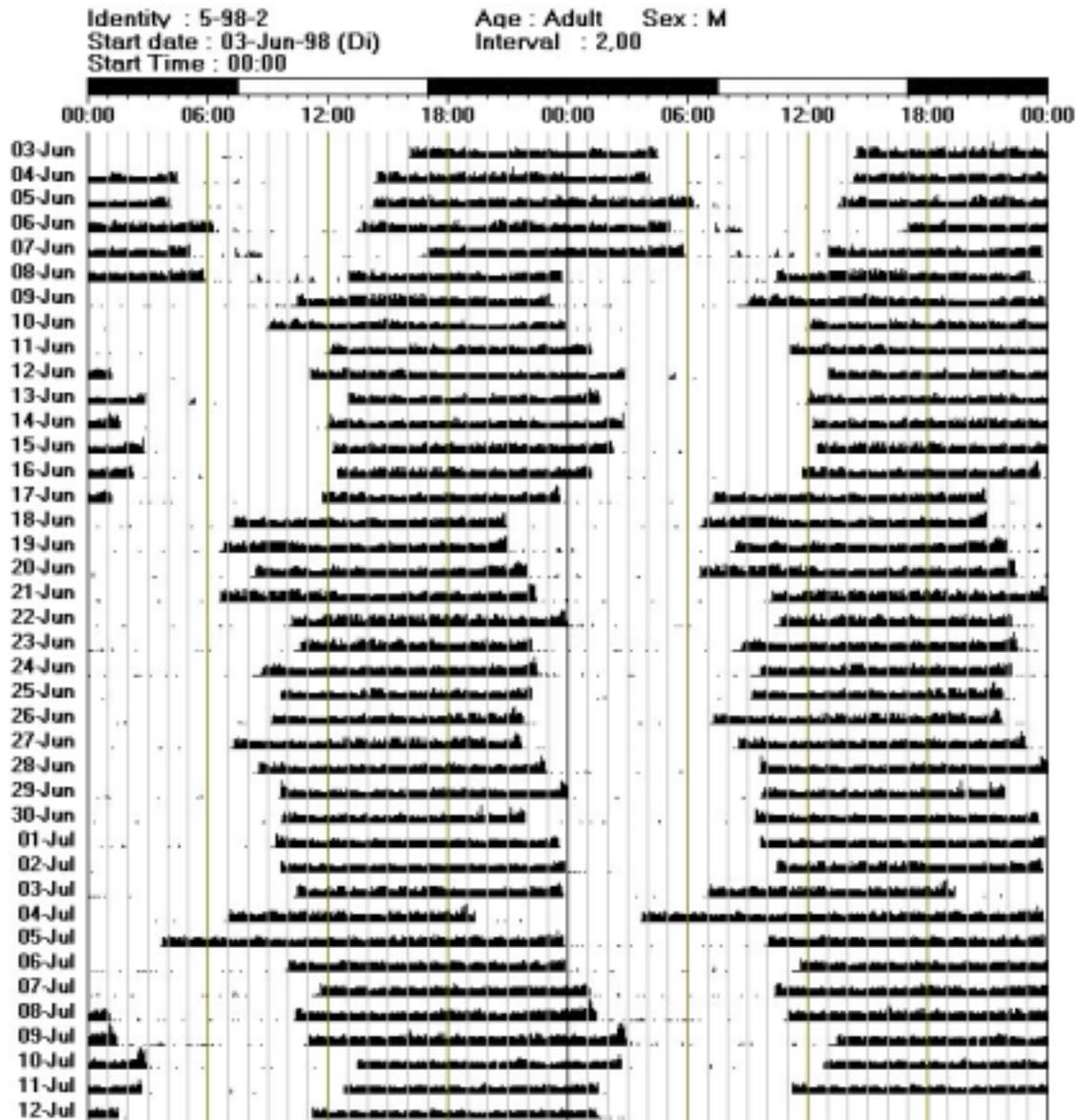
Identity:	04-98-4, Male, subadult , Tag-No. 01C6-11AC, resident
Season	Autumn
Activity pattern	Nocturnal, Period 24 h (p<0.0025)
Site Type	Creek (Lea River)
Details	1.55 kg, Tail fat: 2, Bill: 49/57/81 mm, Body Length: 54 cm, Spur Class: C, Moulting class: light
Data logger	activity logger, AW 530044
Repeat	no



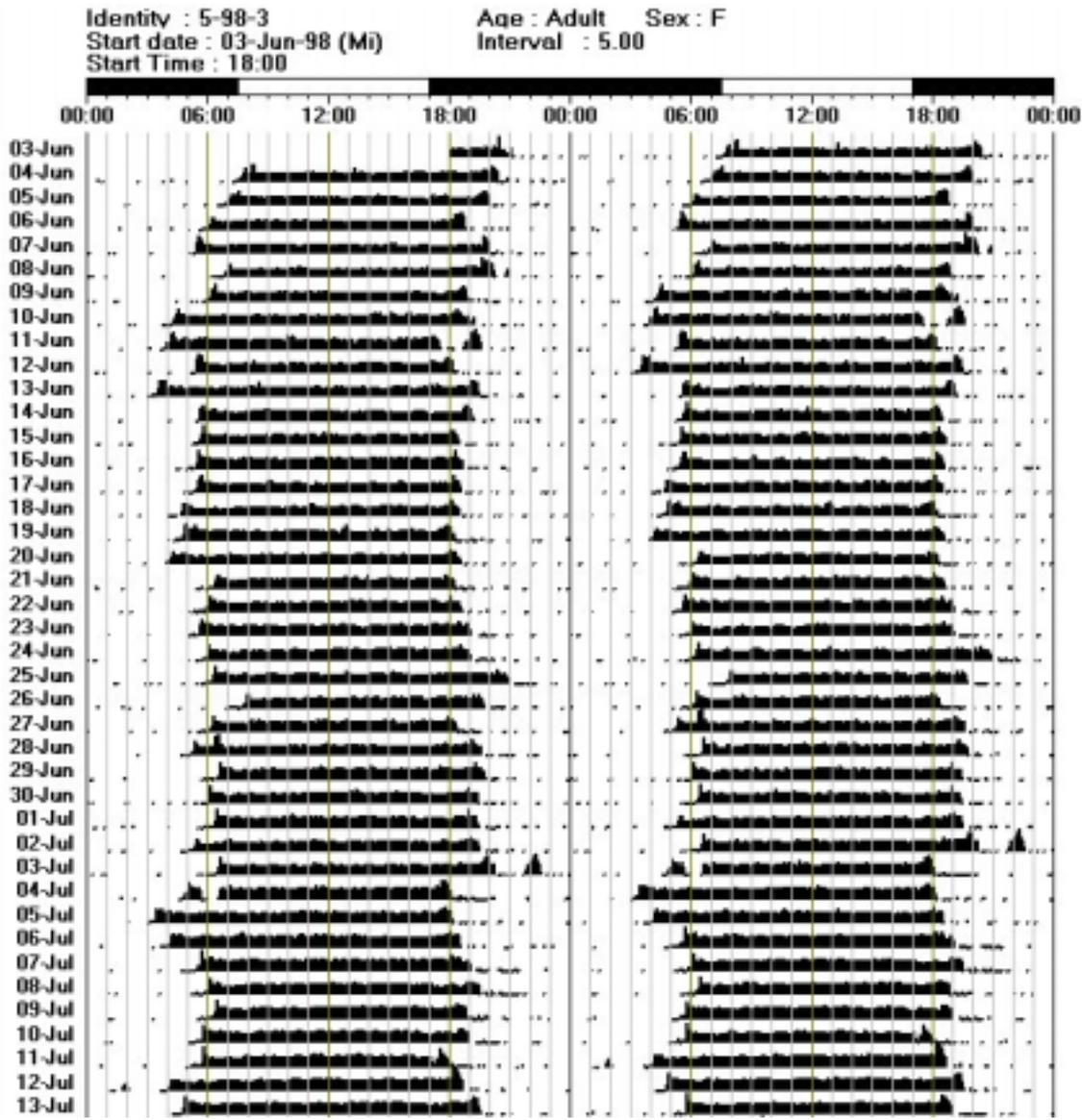
Identity:	04-98-5, Female, adult , Tag-No. 0075-FB2C, resident
Season	Autumn
Activity pattern	Nocturnal, Period 24 h (p<0.0025)
Site Type	Lake (Deep Hole)
Details	1.52 kg, Tail fat: 3, Bill: 47/52/76 mm, Body Length: 54 cm, Spur Class: 0, Moulting class: light
Data logger	activity logger, AW 530048
Repeat	yes, 06-99-6 (TDR)



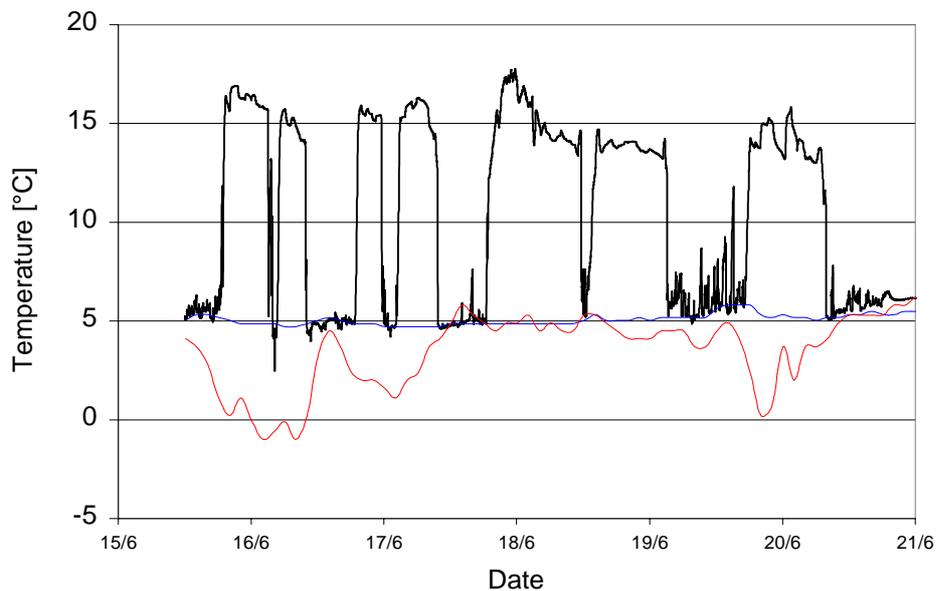
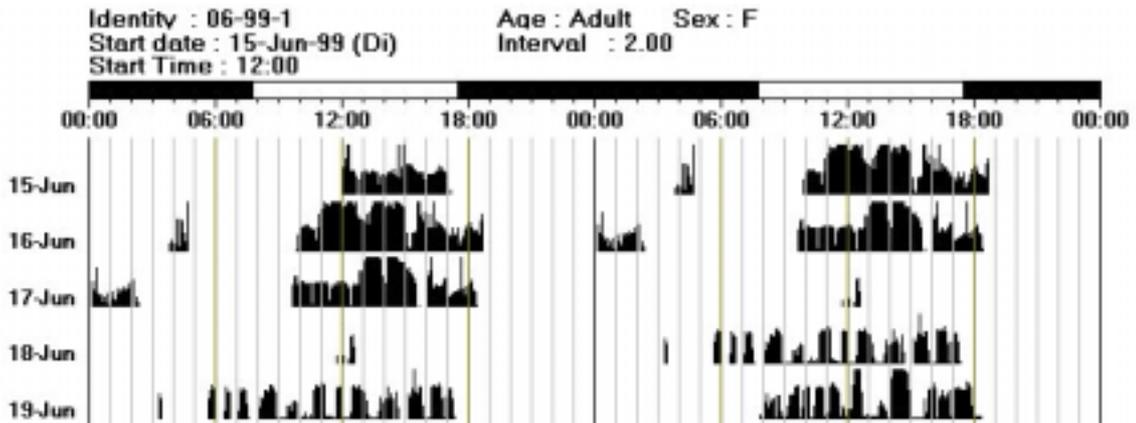
Identity:	05-98-2, Male, adult , Tag-No. 0064-604D, resident
Season	Winter
Activity pattern	Mixed, Period 23.7 (p<0.0061)
Site Type	Lake (Deep Hole)
Details	2.60 kg, Tail fat: 2, Bill: 54/54/71 mm, Body Length: 57 cm, Spur Class: E, Moulting class: none
Data logger	activity logger, AW 511438
Repeat	yes, 06-99-2 (TDR)



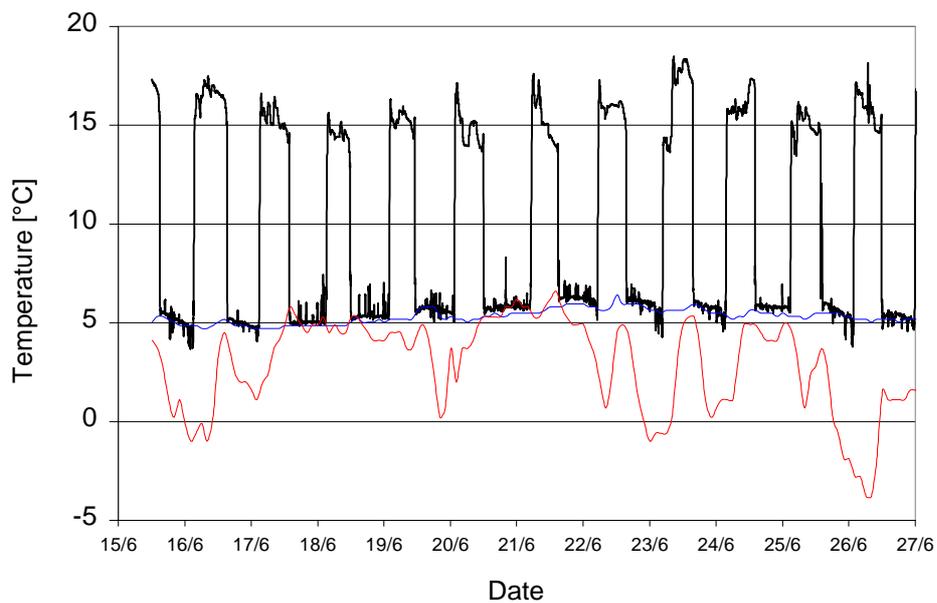
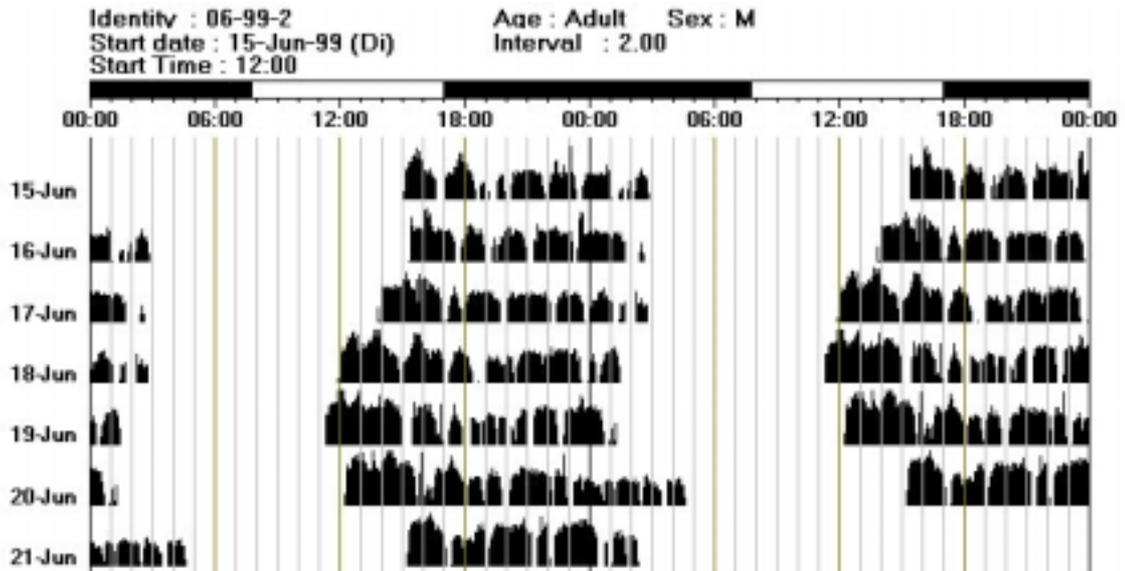
Identity:	05-98-3, Female, adult , Tag-No. 0064-58E1, resident
Season	Winter
Activity pattern	Diurnal, Period 24 h (p<0.0025)
Site Type	Creek (Lea River → Forest Rivulet)
Details	1.55 kg, Tail fat: 2, Bill: 47/55/77 mm, Body Length: 49 cm, Spur Class: 0, Moulting class: very light
Data logger	activity logger, AW 530048
Repeat	no



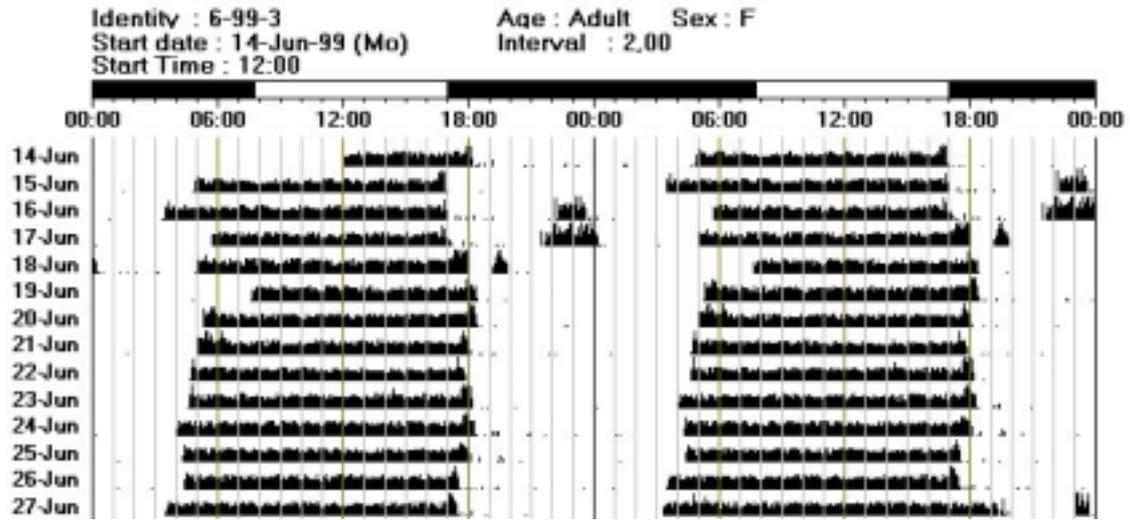
Identity:	06-99-1, Female, adult, Tag-No. 01C6-2F84, resident
Season	Winter
Activity pattern	Diurnal, Period 23 h (p<0.0061)
Site Type	Lake (Deep Hole → Platypus Playground)
Details	1.41 kg, Tail fat: 3, Bill: 45/54/71 mm, Body Length: 49.5 cm, Spur Class: 0, Moulting Class: light
Data logger	time-depth recorder, TDR 2268
Repeat	no



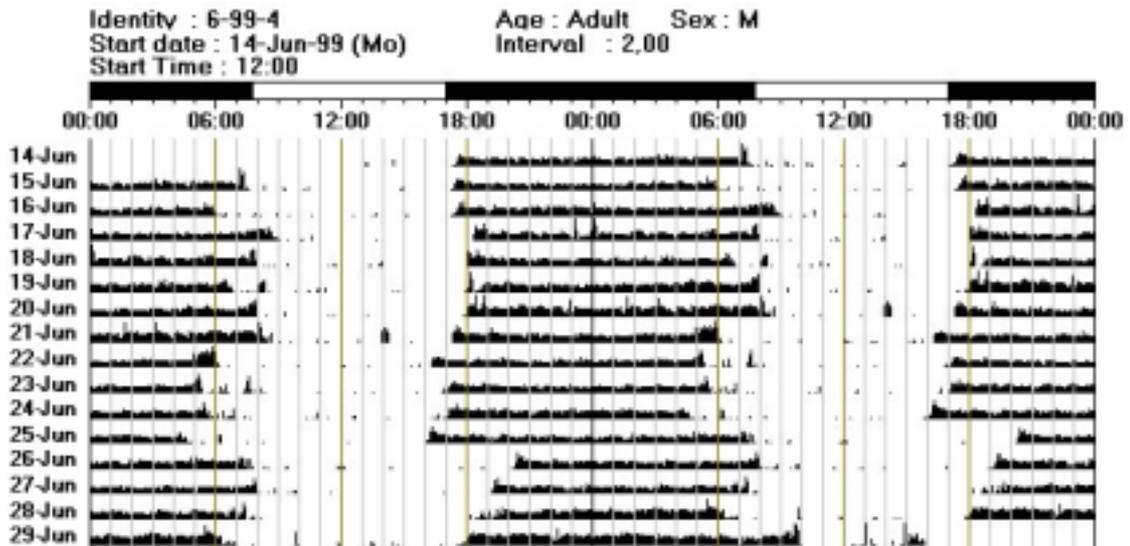
Identity:	06-99-2, Male, adult, Tag-No. 0064-604D, resident
Season	Winter
Activity pattern	Mixed, Period 23.4 h ($p < 0.0061$)
Site Type	Lake (Deep Hole)
Details	2.63 kg, Tail fat: 2, Bill: 54/61/76 mm, Body Length: 61 cm, Spur Class: E, Moulting Class: very light
Data logger	time-depth recorder, TDR 2282
Repeat	yes, 05-98-2 (AL)



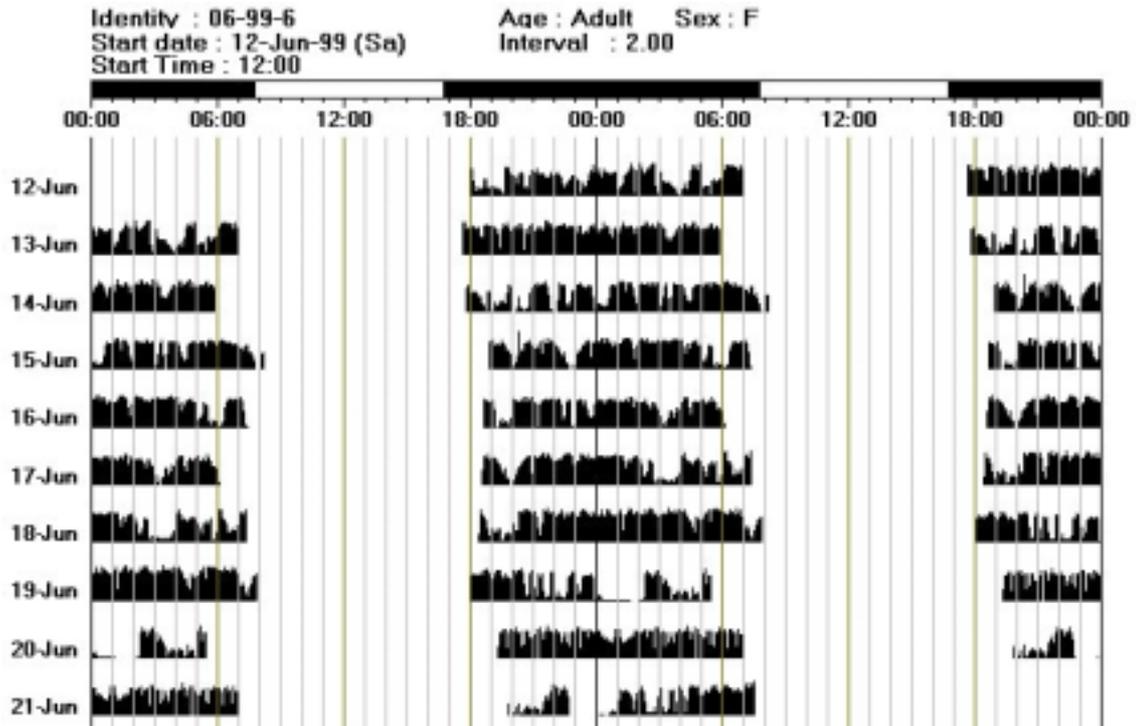
Identity:	06-99-3, Female, adult , Tag-No. 00F6-438A, resident
Season	Winter
Activity pattern	Diurnal, Period 24 h (p<0.0061)
Site Type	Lake (Deep Hole)
Details	1.51 kg, Tail fat: 3, Bill: 44/54/71 mm, Body Length: 49 cm, Spur Class: 0, Moulting class: none
Data logger	activity logger, AW 511914
Repeat	yes, 12-99-1 (TDR)



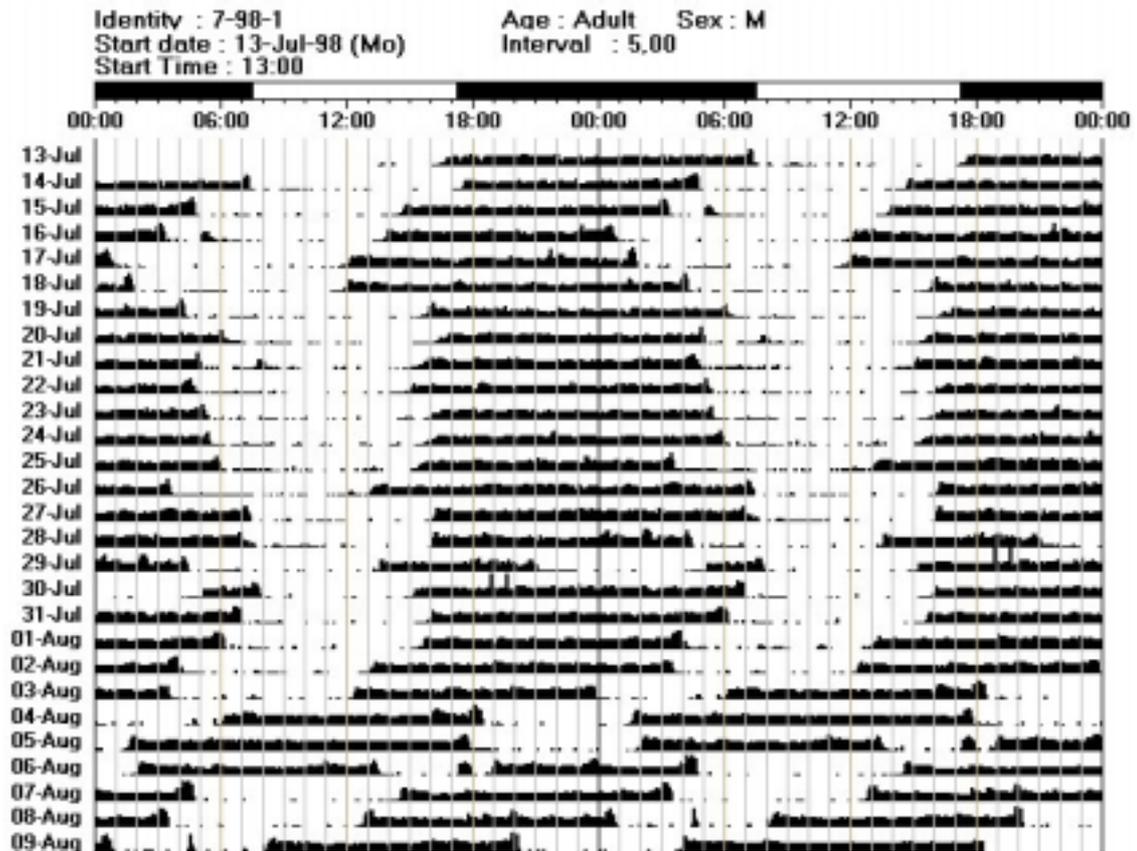
Identity:	06-99-4, Male, adult , Tag-No. 0070-B623, resident
Season	Winter
Activity pattern	Nocturnal, Period 24 h (p<0.0061)
Site Type	Lake (Deep Hole)
Details	2.07 kg, Tail fat: 2, Bill: 50/59/80 mm, Body Length: 55 cm, Spur Class: E, Moulting class: moderate
Data logger	activity logger, AW 530048
Repeat	no



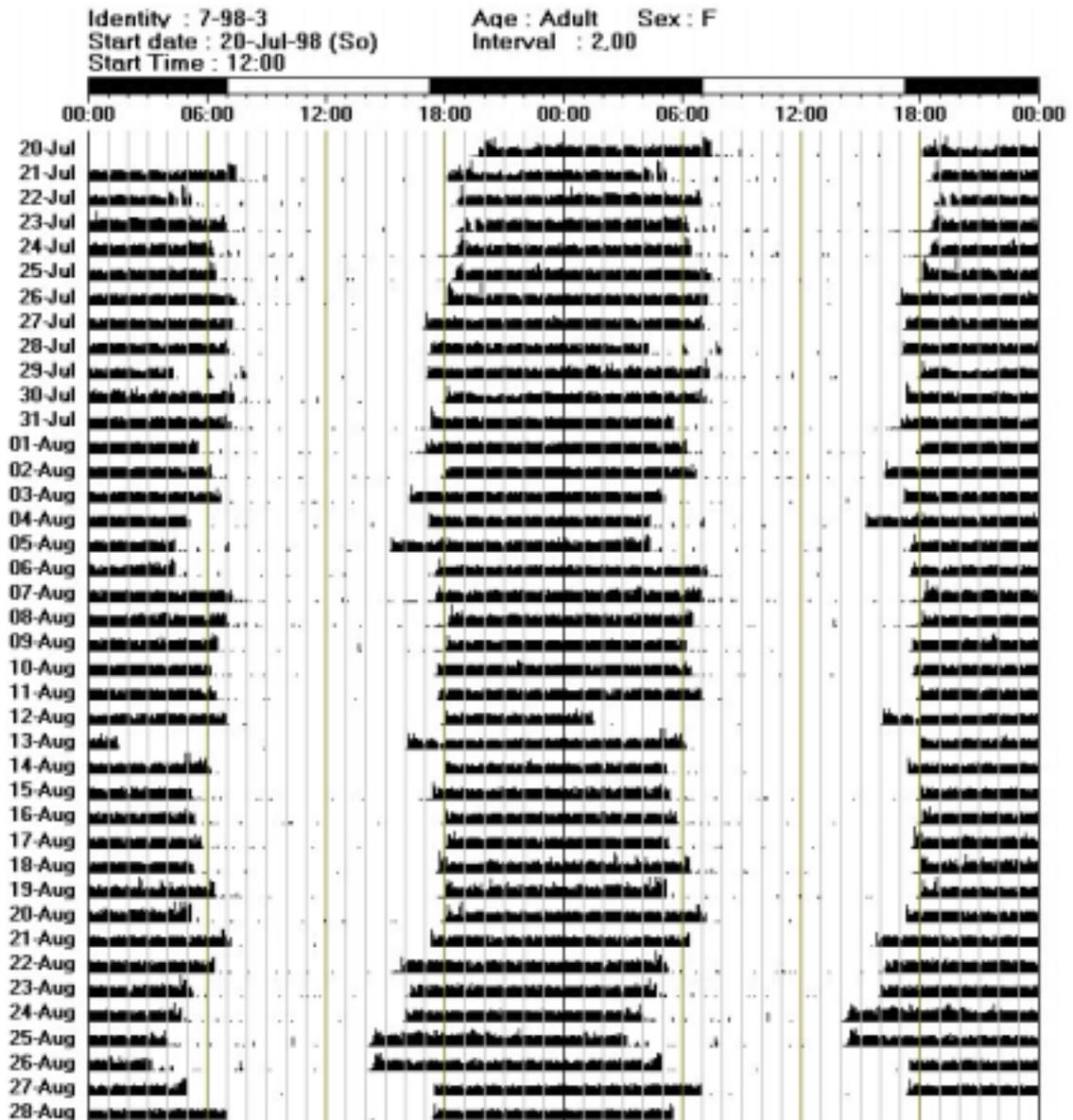
Identity:	06-99-6, Female, adult, Tag-No. 0075-FB2C, resident
Season	Winter
Activity pattern	Nocturnal, Period 24.1 h ($p < 0.0061$)
Site Type	Lake (Deep Hole)
Details	1.54 kg, Tail fat: 3, Bill: 46/56/77 mm, Body Length: 55 cm, Spur Class: 0, Moulting Class: moderate
Data logger	time-depth recorder, TDR 1995
Repeat	yes, 04-98-5 (AL)



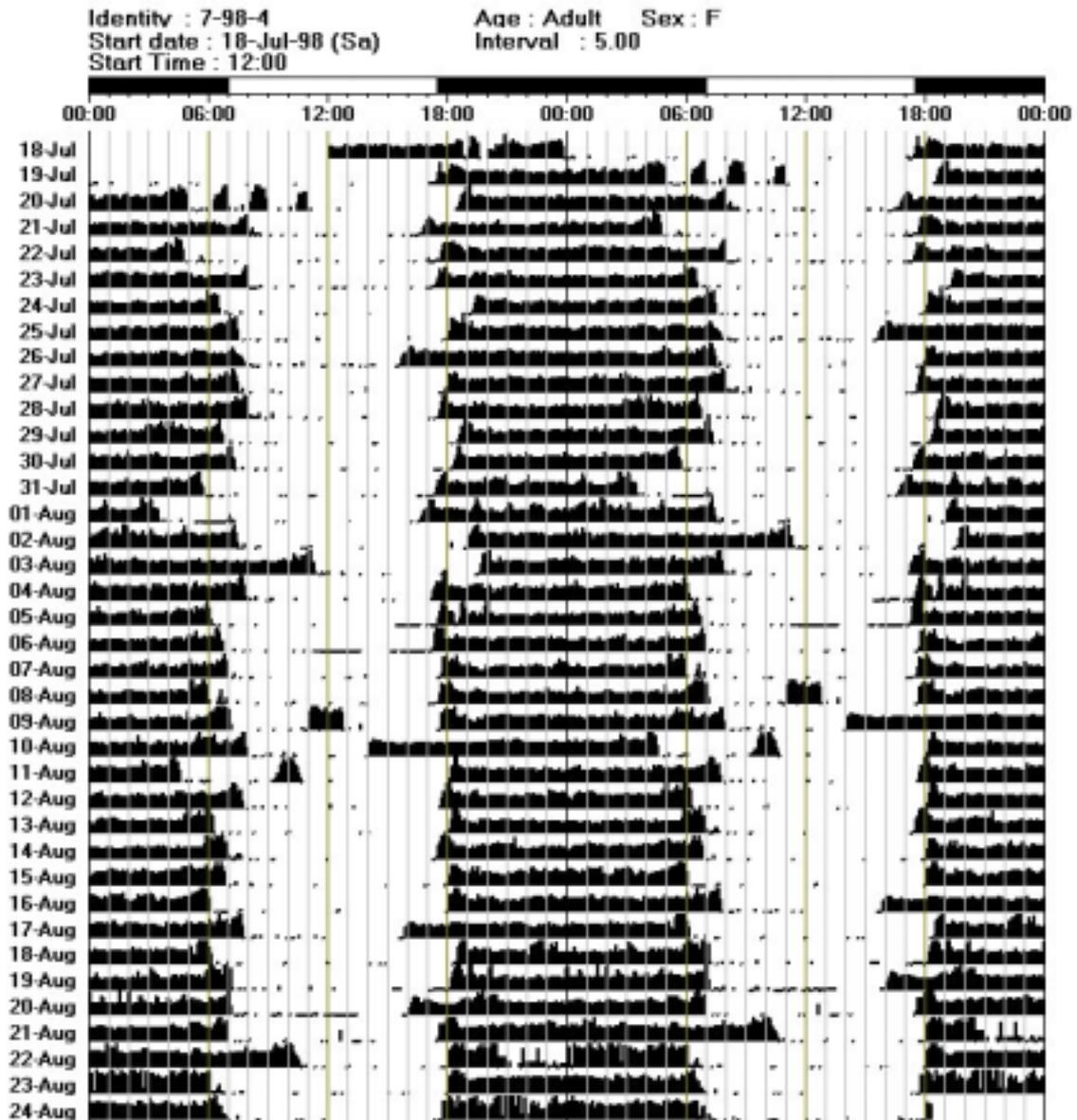
Identity:	07-98-1, Male, adult , Tag-No. 0075-F6B7, transient
Season	Winter
Activity pattern	Mixed, Period 24 h ($p < 0.0025$)
Site Type	Lake (Deep Hole)
Details	1.93 kg, Tail fat: 3, Bill: 52/58/77 mm, Body Length: 56 cm, Spur Class: D, Moulting class: very light
Data logger	activity logger, AW 530044
Repeat	no



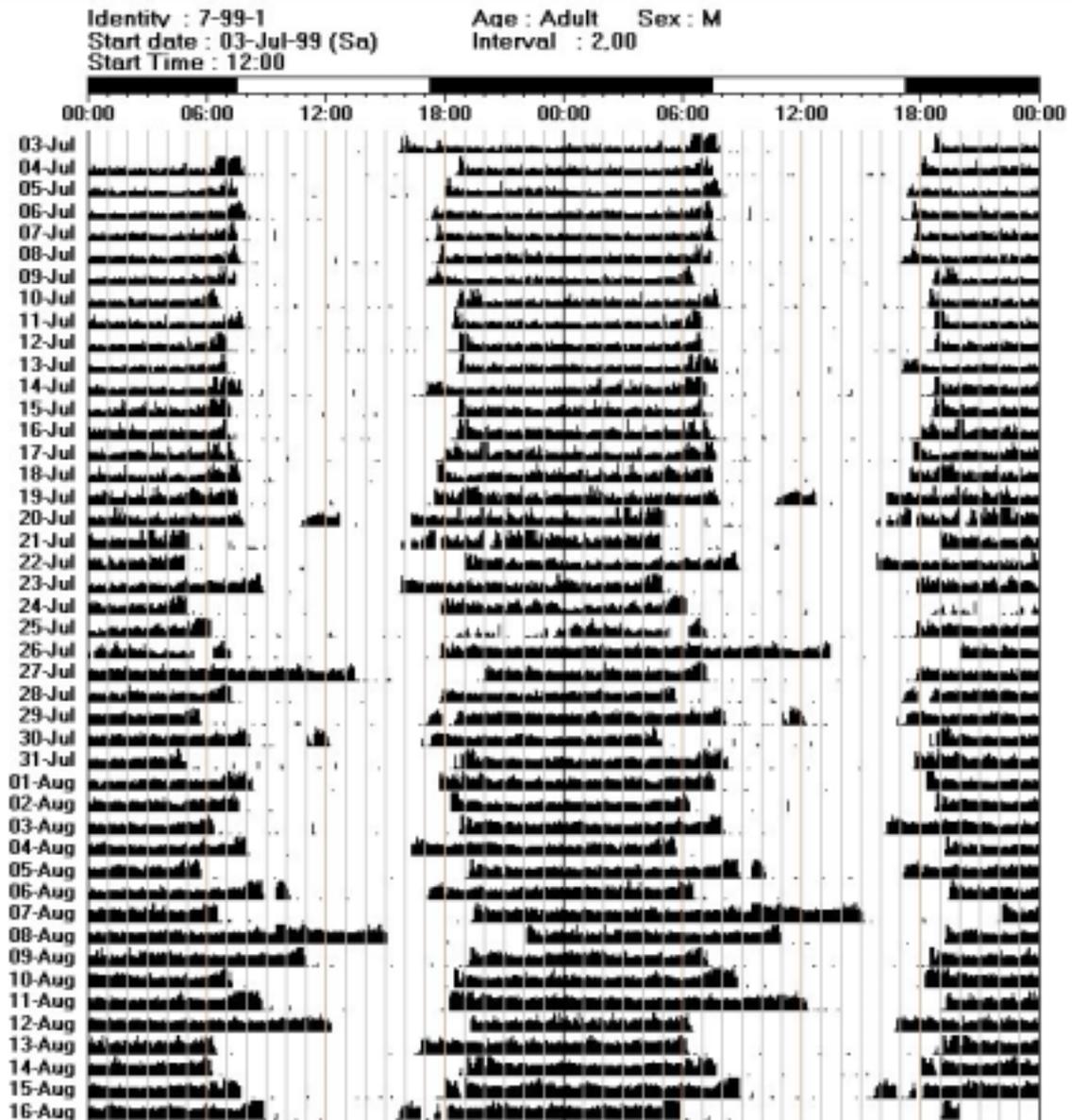
Identity:	07-98-3, Female, adult , Tag-No. 01D1-F70D, resident
Season	Winter
Activity pattern	Nocturnal, Period 23.9 h ($p < 0.0061$)
Site Type	Creek (Jennifer Creek)
Details	1.43 kg, Tail fat: 3, Bill: 45/54/71 mm, Body Length: 52 cm, Spur Class: 0, Moulting class: very light
Data logger	activity logger, AW 511438
Repeat	no



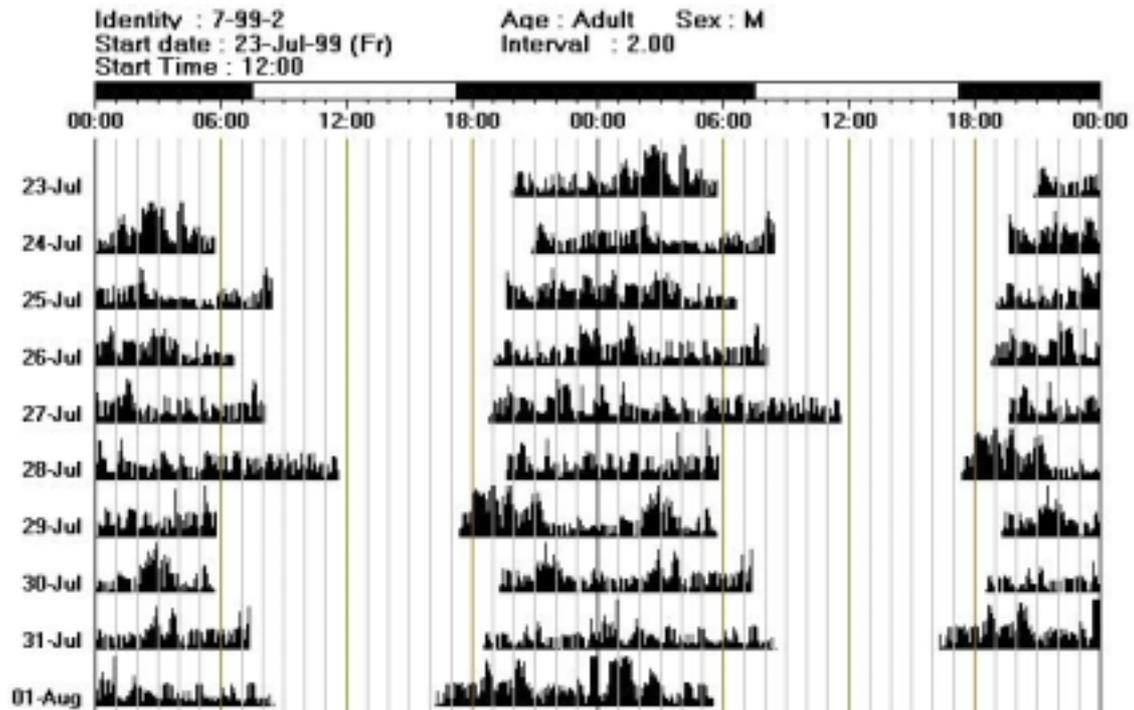
Identity:	07-98-4, Female, adult , Tag-No. 00F6-3DCC, resident
Season	Winter
Activity pattern	Nocturnal, Period 24 h (p<0.0025)
Site Type	Creek (Bare Mount Creek)
Details	1.13 kg, Tail fat: 2, Bill: 42/48/68 mm, Body Length: 48 cm, Spur Class: 0, Moulting class: very light
Data logger	activity logger, AW 530048
Repeat	no



Identity:	07-99-1, Male, adult , Tag-No. 0064-5E20, resident
Season	Winter
Activity pattern	Nocturnal, Period 24 h (p<0.0061)
Site Type	Creek (Jennifer Creek)
Details	2.61 kg, Tail fat: 2, Bill: 50/61/82 mm, Body Length: 59 cm, Spur Class: E, Moul class: moderate
Data logger	activity logger, AW 511687
Repeat	no



Identity:	07-99-2, Male, adult, Tag-No. 01D0-CCAD, resident
Season	Winter
Activity pattern	Nocturnal, Period 23.7 h ($p < 0.0061$)
Site Type	Creek (Jennifer Creek)
Details	1.68 kg, Tail fat: 3, Bill: 45/55/74 mm, Body Length: 51 cm, Spur Class: E, Moulting Class: light
Data logger	time-depth recorder, TDR 2282
Repeat	yes, 01-00-3 (AL)



Appendix B-1: Platypus Energetics: Statistics**Rest in Air**ANALYSIS OF VARIANCEDEP VAR: **P(REST IN AIR)**, N: 14, MULTIPLE R: 0.955, SQUARED MULTIPLE R: 0.911

CATEGORICAL VALUES ENCOUNTERED DURING PROCESSING ARE:

ANIMAL (10 LEVELS): A, B, C, E, F, G, H, I, J, L

<i>SOURCE</i>	<i>SUM-OF-SQUARES</i>	<i>DF</i>	<i>MEAN-SQUARE</i>	<i>F-RATIO</i>	<i>P</i>
ANIMAL	0.340	9	0.038	0.465	0.000
AIR TEMP	0.160	1	0.160	1.970	0.000
WEIGHT	0.028	1	0.028	0.350	0.052
ERROR	0.163	2	0.081		

Rest in WaterANALYSIS OF VARIANCEDEP VAR: **P(REST IN WATER)**, N: 47, MULTIPLE R: 0.838, SQUARED MULTIPLE R: 0.703

CATEGORICAL VALUES ENCOUNTERED DURING PROCESSING ARE:

ANIMAL (10 LEVELS): A, C, D, E, F, G, H, I, J, L

<i>SOURCE</i>	<i>SUM-OF-SQUARES</i>	<i>DF</i>	<i>MEAN-SQUARE</i>	<i>F-RATIO</i>	<i>P</i>
ANIMAL	6.271	9	0.697	1.450	0.000
WATER TEM	0.024	1	0.024	0.051	0.000
WEIGHT	0.016	1	0.016	0.033	0.725
ERROR	16.822	35	0.481		

Metabolic rate of diving and foraging in the swim tankANALYSIS OF VARIANCEDEP VAR: **P(TOTAL)**, N: 555, MULTIPLE R: 0.748, SQUARED MULTIPLE R: 0.559

CATEGORICAL VALUES ENCOUNTERED DURING PROCESSING ARE:

ANIMAL\$ (12 LEVELS): A, B, C, D, E, F, G, H, I, J, K, L

<i>SOURCE</i>	<i>SUM-OF-SQUARES</i>	<i>DF</i>	<i>MEAN-SQUARE</i>	<i>F-RATIO</i>	<i>P</i>
ANIMAL	175970.250	11	15997.295	6.843	0.000
WATER TEMP	22128.812	1	22128.812	9.466	0.002
WEIGHT	47271.198	1	47271.198	20.222	0.000
DIVE DURATION	1377605.855	1	1377605.855	589.325	0.000
ERROR	1262304.137	540	2337.600		

MIXED REGRESSIONDEP VAR: **P(TOTAL)**, 2 RANDOM TERMS, **DIVE DURATION, WATER TEMP**, 2 FIXED TERMS, **WEIGHT, INTERCEPT**

LEVEL 2 OBSERVATIONS = 12, LEVEL 1 OBSERVATIONS = 555

BETWEEN SUBJECTS:

<i>VARIABLE</i>	<i>ESTIMATE</i>	<i>STANDARDIZED ERROR</i>	<i>Z</i>	<i>P-VALUE</i>
DIVE DURATION	-0.246	0.028	-8.950	0.000
WATER TEMP	-0.158	0.080	-1.980	0.048
WEIGHT	-1.177	0.500	-2.356	0.018
INTERCEPT	19.426	1.221	15.908	0.000

WITHIN SUBJECTS: RANDOM-EFFECT VARIANCE & COVARIANCE TERM(S):

ESTIMATE

	<i>DIVE DURATION</i>	<i>WATER TEMP</i>
DIVE DURATION	0.007	
WATER TEMP	-0.013	0.025

STANDARDIZED ERROR

	<i>DIVE DURATION</i>	<i>WATER TEMP</i>
DIVE DURATION	0.004	
WATER TEMP	0.007	0.013

Z

	<i>DIVE DURATION</i>	<i>WATER TEMP</i>
DIVE DURATION	1.882	
WATER TEMP	-1.849	1.849

P-VALUE

	<i>DIVE DURATION</i>	<i>WATER TEMP</i>
DIVE DURATION	0.030	
WATER TEMP	0.064	0.032

NONLINEAR REGRESSION

MODEL: P(FORAGE) = A + B X WATER TEMP + C X WEIGHT + D / DIVE DURATION

<i>SOURCE</i>	<i>SUM-OF-SQUARES</i>	<i>DF</i>	<i>MEAN-SQUARE</i>
REGRESSION	69277.596	4	17319.399
RESIDUAL	3271.770	551	5.938
TOTAL	72549.366	555	
MEAN CORRECTED	8437.650	554	

RAW R-SQUARE (1-RESIDUAL/TOTAL) = 0.955

MEAN CORRECTED R-SQUARE (1-RESIDUAL/CORRECTED) = 0.612

R(OBSERVED VS PREDICTED) SQUARE = 0.612

<i>PARAMETER</i>	<i>ESTIMATE</i>
A	9.035
B	-0.205
C	-0.899
D	109.210

Cost of transport

REGRESSION

DEP VAR: COT N: 119 MULTIPLE R: 0.658 SQUARED MULTIPLE R: 0.432

ADJUSTED SQUARED MULTIPLE R: .428 STANDARD ERROR OF ESTIMATE: 1.690

<i>VARIABLE</i>	<i>COEF</i>	<i>STD ERROR</i>	<i>STD COEF</i>	<i>TOLERANCE</i>	<i>T</i>	<i>P (2 TAIL)</i>
CONSTANT	8.185	0.470	0.000		17.431	0.000
SWIM SPEED	-20.292	2.149	-0.658	1.000	-9.441	0.000

ANALYSIS OF VARIANCE

<i>SOURCE</i>	<i>SUM-OF-SQUARES</i>	<i>DF</i>	<i>MEAN-SQUARE</i>	<i>F-RATIO</i>	<i>P</i>
REGRESSION	254.483	1	254.483	89.140	0.000
RESIDUAL	334.019	117	2.855		

NONLINEAR REGRESSION

MODEL: $P(\text{DIVE}) = A \times \text{SWIM SPEED}^3 + B \times \text{SWIM SPEED}^2 + C \times \text{SWIM SPEED} + P(\text{REST IN WATER})$

<i>SOURCE</i>	<i>SUM-OF-SQUARES</i>	<i>DF</i>	<i>MEAN-SQUARE</i>
REGRESSION	196.225	3	65.408
RESIDUAL	0.028	1	0.028
TOTAL	196.059	4	
MEAN CORRECTED	0.276	3	

RAW R-SQUARED (1-RESIDUAL/TOTAL) = 1.000
 CORRECTED R-SQUARED (1-RESIDUAL/CORRECTED) = 0.898

<i>PARAMETER</i>	<i>ESTIMATE</i>
A	236.142
B	-167.844
C	35.504

NONLINEAR REGRESSION

COMPARISON OF COT, DEPENDENT VARIABLE IS **COT**

<i>SOURCE</i>	<i>SUM-OF-SQUARES</i>	<i>DF</i>	<i>MEAN-SQUARE</i>
REGRESSION	7.038	2	3.519
RESIDUAL	0.026	2	0.013
TOTAL	7.064	4	
CORRECTED	0.738	3	

RAW R-SQUARED (1-RESIDUAL/TOTAL) = 0.996
 CORRECTED R-SQUARED (1-RESIDUAL/CORRECTED) = 0.965

<i>PARAMETER</i>	<i>ESTIMATE</i>
A	2.124
B	-0.373

Appendix B-2: Behavioural activity of the Platypus: Statistics**Diving behaviour**ANALYSIS OF VARIANCEDEP VAR: **DIVE DURATION** N: 88905 MULTIPLE R: 0.677 SQUARED MULTIPLE R: 0.459

CATEGORICAL VALUES ENCOUNTERED DURING PROCESSING ARE:

ANIMAL (14 LEVELS): A, B, C, D, E, F, G, H, I, J, K, L, M, N

<i>SOURCE</i>	<i>SUM-OF-SQUARES</i>	<i>DF</i>	<i>MEAN-SQUARE</i>	<i>F-RATIO</i>	<i>P</i>
ANIMAL	833533.057	13	83353.306	1039.660	0.000
DIVE DEPTH	4380942.231	1	4380942.231	54643.211	0.000
ERROR	7126870.715	88891	80.174		

ANALYSIS OF VARIANCEDEP VAR: **SURFACE DURATION** N: 86658 MULTIPLE R: 0.421 SQUARED MULTIPLE R: 0.178

CATEGORICAL VALUES ENCOUNTERED DURING PROCESSING ARE:

ANIMAL (14 LEVELS): A, B, C, D, E, F, G, H, I, J, K, L, M, N

<i>SOURCE</i>	<i>SUM-OF-SQUARES</i>	<i>DF</i>	<i>MEAN-SQUARE</i>	<i>F-RATIO</i>	<i>P</i>
ANIMAL	239734.213	13	18441.093	628.277	0.000
DIVE DURATION	183437.195	1	183437.195	6249.598	0.000
ERROR	2543131.196	86643	29.352		

ANALYSIS OF VARIANCEDEP VAR: **DIVE DURATION** N: 14 MULTIPLE R: 0.881 SQUARED MULTIPLE R: 0.777

<i>SOURCE</i>	<i>SUM-OF-SQUARES</i>	<i>DF</i>	<i>MEAN-SQUARE</i>	<i>F-RATIO</i>	<i>P</i>
SEX	53.788	1	53.788	8.906	0.017
SEASON	58.409	2	29.205	4.836	0.042
SEX*SEASON	12.060	2	6.030	0.998	0.410
ERROR	48.315	8	6.039		

ANALYSIS OF VARIANCEDEP VAR: **SURFACE DURATION** N: 14 MULTIPLE R: 0.877 SQUARED MULTIPLE R: 0.769

<i>SOURCE</i>	<i>SUM-OF-SQUARES</i>	<i>DF</i>	<i>MEAN-SQUARE</i>	<i>F-RATIO</i>	<i>P</i>
SEX	12.199	1	12.199	8.190	0.021
SEASON	22.657	2	11.329	7.606	0.014
SEX*SEASON	11.683	2	5.841	3.922	0.065
ERROR	11.915	8	1.489		

ANALYSIS OF VARIANCEDEP VAR: **DIVE DEPTH** N: 11 MULTIPLE R: 0.936 SQUARED MULTIPLE R: 0.875

<i>SOURCE</i>	<i>SUM-OF-SQUARES</i>	<i>DF</i>	<i>MEAN-SQUARE</i>	<i>F-RATIO</i>	<i>P</i>
SEASON	0.793	1	0.793	26.249	0.001
SEX	0.563	1	0.563	18.626	0.003
SEASON*SEX	0.232	1	0.232	7.669	0.028
ERROR	0.212	7	0.030		

ANALYSIS OF VARIANCEDEP VAR: **DIVE DURATION** N: 1095 MULTIPLE R: 0.594 SQUARED MULTIPLE R: 0.353

CATEGORICAL VALUES ENCOUNTERED DURING PROCESSING ARE:

ANIMAL (11 LEVELS): A, B, C, D, E, F, G, H, I, J, K

<i>SOURCE</i>	<i>SUM-OF-SQUARES</i>	<i>DF</i>	<i>MEAN-SQUARE</i>	<i>F-RATIO</i>	<i>P</i>
ANIMAL	23896.070	10	2389.607	53.785	0.000
WATERTEMP	487.400	1	487.400	10.970	0.001
P	794.643	1	794.643	17.886	0.000
AIRTEMP	48071.674	1082	44.429		
ERROR					

ANALYSIS OF VARIANCEDEP VAR: **NUMBER OF DIVES PER HOUR** N: 1095 MULTIPLE R: 0.386 SQUARED MULTIPLE

R: 0.149

<i>SOURCE</i>	<i>SUM-OF-SQUARES</i>	<i>DF</i>	<i>MEAN-SQUARE</i>	<i>F-RATIO</i>	<i>P</i>
SEX	6308.208	1	6308.208	19.389	0.000
SEASON	6663.985	1	6663.985	20.483	0.000
LIGHT LEVELS	3841.199	2	1920.599	5.903	0.003
SEX*SEASON	577.297	1	577.297	1.774	0.183
SEX*LIGHT LEVELS	655.164	2	327.582	1.007	0.366
SEASON*LIGHT LEVELS	1107.180	2	553.590	1.702	0.183
SEX*SEASON*LIGHT LEVELS	191.452	2	95.726	0.294	0.745
ERROR	352345.368	1083	325.342		

ANALYSIS OF VARIANCEDEP VAR: **DIVE DURATION** N: 1095 MULTIPLE R: 0.678 SQUARED MULTIPLE R: 0.460

<i>SOURCE</i>	<i>SUM-OF-SQUARES</i>	<i>DF</i>	<i>MEAN-SQUARE</i>	<i>F-RATIO</i>	<i>P</i>
LIGHT LEVELS	6527.095	2	3263.548	88.161	0.000
SEX	4124.872	1	4124.872	111.428	0.000
SEASON	0.153	1	0.153	0.004	0.049
LIGHT LEVELS*SEX	330.447	2	165.224	4.463	0.012
LIGHT LEVELS*SEASON	3469.176	2	1734.588	46.858	0.000
SEX*SEASON	103.694	1	103.694	2.801	0.094
LIGHT LEVELS*SEX*SEASON	430.173	2	215.087	5.810	0.003
ERROR	40090.732	1083	37.018		

ANALYSIS OF VARIANCEDEP VAR: **SURFACE DURATION** N: 1095 MULTIPLE R: 0.609 SQUARED MULTIPLE R: 0.371

<i>SOURCE</i>	<i>SUM-OF-SQUARES</i>	<i>DF</i>	<i>MEAN-SQUARE</i>	<i>F-RATIO</i>	<i>P</i>
LIGHT LEVELS	77.454	2	38.727	5.762	0.003
SEX	759.300	1	759.300	112.978	0.000
SEASON	484.973	1	484.973	72.160	0.000
LIGHT LEVELS*SEX	0.273	2	0.137	0.020	0.980
LIGHT LEVELS*SEASON	19.002	2	9.501	1.414	0.244
SEX*SEASON	89.255	1	89.255	13.280	0.000
LIGHT LEVELS*SEX*SEASON	58.323	2	29.161	4.339	0.013
ERROR	7278.608	1083	6.721		

ANALYSIS OF VARIANCEDEP VAR: **DIVE DEPTH** N: 1095 MULTIPLE R: 0.726 SQUARED MULTIPLE R: 0.528

<i>SOURCE</i>	<i>SUM-OF-SQUARES</i>	<i>DF</i>	<i>MEAN-SQUARE</i>	<i>F-RATIO</i>	<i>P</i>
LIGHT LEVELS	39.881	2	19.941	88.505	0.000
SEX	27.256	1	27.256	120.974	0.000
SEASON	12.117	1	12.117	53.779	0.000
LIGHT LEVELS*SEX	0.043	2	0.021	0.094	0.910
LIGHT LEVELS*SEASON	16.447	2	8.223	36.499	0.000
SEX*SEASON	10.476	1	10.476	46.495	0.000
LIGHT LEVELS*SEX*SEASON	2.856	2	1.428	6.338	0.002
ERROR	244.004	1083	0.225		

*Foraging behaviour*ANALYSIS OF VARIANCEDEP VAR: **FORAGING DURATION (TDR-DATA)** N: 11 MULTIPLE R: 0.266 SQUARED MULTIPLE R: 0.071

<i>SOURCE</i>	<i>SUM-OF-SQUARES</i>	<i>DF</i>	<i>MEAN-SQUARE</i>	<i>F-RATIO</i>	<i>P</i>
SEASON	18.575	1	18.575	4.312	0.041
SEX	6.371	1	6.371	1.479	0.227
SEASON*SEX	2.970	1	2.970	0.690	0.408
ERROR	387.661	7	4.307		

ANALYSIS OF VARIANCEDEP VAR: **FORAGING DURATION (AL-DATA)** N: 24 MULTIPLE R: 0.191 SQUARED MULTIPLE R: 0.036

<i>SOURCE</i>	<i>SUM-OF-SQUARES</i>	<i>DF</i>	<i>MEAN-SQUARE</i>	<i>F-RATIO</i>	<i>P</i>
SEASON	209.439	3	69.813	9.110	0.000
SEX	11.281	1	11.281	1.425	0.233
ERROR	5533.206	19	7.664		

ANALYSIS OF VARIANCEDEP VAR: **ACTIVE PERIOD (AL-DATA)** N: 24 MULTIPLE R: 0.191 SQUARED MULTIPLE R: 0.036

<i>SOURCE</i>	<i>SUM-OF-SQUARES</i>	<i>DF</i>	<i>MEAN-SQUARE</i>	<i>F-RATIO</i>	<i>P</i>
SEASON	228.833	3	76.278	9.106	0.000
SEX	1.804	1	1.804	0.208	0.648
ERROR	6047.873	19	8.377		

ANALYSIS OF VARIANCEDEP VAR: **FORAGING DURATION (TDR-DATA)** N: 98 MULTIPLE R: 0.655 SQUARED MULTIPLE R: 0.429CATEGORICAL VALUES ENCOUNTERED DURING PROCESSING ARE:
ANIMAL (11 LEVELS)

<i>SOURCE</i>	<i>SUM-OF-SQUARES</i>	<i>DF</i>	<i>MEAN-SQUARE</i>	<i>F-RATIO</i>	<i>P</i>
ANIMAL	113.065	9	12.563	4.431	0.000
WATER TEMP	1.460	1	1.460	0.515	0.475
AIR TEMP	4.929	1	4.929	1.739	0.191
ERROR	209.803	86	2.835		

ANALYSIS OF VARIANCEDEP VAR: **FORAGING DURATION (AL-DATA)** N: 726 MULTIPLE R: 0.398 SQUARED

MULTIPLE R: 0.158

CATEGORICAL VALUES ENCOUNTERED DURING PROCESSING ARE:

ANIMAL (24 LEVELS)

<i>SOURCE</i>	<i>SUM-OF-SQUARES</i>	<i>DF</i>	<i>MEAN-SQUARE</i>	<i>F-RATIO</i>	<i>P</i>
ANIMAL	633.138	24	26.381	3.536	0.000
AIR TEMP	0.026	1	0.026	0.003	0.953
WATER TEMP	2.470	1	2.470	0.331	0.565
ERROR	4670.822	699	7.461		

ANALYSIS OF VARIANCEDEP VAR: **DAILY ACTIVITY** N: 726 MULTIPLE R: 0.687 SQUARED MULTIPLE R: 0.472

CATEGORICAL VALUES ENCOUNTERED DURING PROCESSING ARE:

ANIMAL (24 LEVELS)

<i>SOURCE</i>	<i>SUM-OF-SQUARES</i>	<i>DF</i>	<i>MEAN-SQUARE</i>	<i>F-RATIO</i>	<i>P</i>
ANIMAL	8.76418E+11	23	3.65174E+10	14.119	0.000
WATER TEMP	4.18636E+10	1	4.18636E+10	16.187	0.000
AIR TEMP	7.34346E+07	1	7.34346E+07	0.028	0.866
ERROR	1.52851E+12	700	2.58632E+09		

ANALYSIS OF VARIANCEDEP VAR: **DAILY ACTIVITY** N: 726 MULTIPLE R: 0.697 SQUARED MULTIPLE R: 0.486

CATEGORICAL VALUES ENCOUNTERED DURING PROCESSING ARE:

ANIMAL (24 LEVELS)

<i>SOURCE</i>	<i>SUM-OF-SQUARES</i>	<i>DF</i>	<i>MEAN-SQUARE</i>	<i>F-RATIO</i>	<i>P</i>
ANIMAL	9.15053E+11	23	3.81272E+10	14.900	0.000
MONTH	4.74633E+10	1	4.74633E+10	18.549	0.000
ERROR	1.68370E+12	701	2.55882E+09		

POST HOC TEST OF **DAILY ACTIVITY**

TUKEY HSD MULTIPLE COMPARISONS.

MATRIX OF PAIRWISE COMPARISON PROBABILITIES:

MONTH	1	2	3	4	5	6	7	8	9	10	11	12
1	1.000											
2	0.000	1.000										
3	0.092	0.967	1.000									
4	0.000	0.997	0.573	1.000								
5	0.000	0.473	0.034	0.997	1.000							
6	0.000	0.015	0.000	0.500	0.884	1.000						
7	0.000	0.000	0.000	0.000	0.000	0.142	1.000					
8	0.000	1.000										
9	0.000	0.357	1.000									
10	0.000	0.204	0.018	0.000	0.032	0.000	0.000	0.108	0.891	1.000		
11	0.000	0.000	0.000	0.000	0.000	0.000	0.012	0.998	0.000	0.003	1.000	
12	0.000	0.001	0.000	0.195	0.471	1.000	0.351	0.000	0.000	1.000	0.000	1.000

ANALYSIS OF VARIANCEDEP VAR: **DAILY ACTIVITY** N: 24 MULTIPLE R: 0.035 SQUARED MULTIPLE R: 0.001

<i>SOURCE</i>	<i>SUM-OF-SQUARES</i>	<i>DF</i>	<i>MEAN-SQUARE</i>	<i>F-RATIO</i>	<i>P</i>
SEX	.399303E+10	1	.399303E+10	0.832	0.362
ERROR	.327424E+13	22	.480094E+10		

ANALYSIS OF VARIANCEDEP VAR: **PERCENTAGE OF ACTIVITY** N: 7260 MULTIPLE R: 0.385 SQUARED MULTIPLE R: 0.148

<i>SOURCE</i>	<i>SUM-OF-SQUARES</i>	<i>DF</i>	<i>MEAN-SQUARE</i>	<i>F-RATIO</i>	<i>P</i>
RELATIVE TIME OF TRIP	2949.898	9	327.766	140.145	0.000
ERROR	16956.051	7250	2.339		

POST HOC TEST OF **PERCENTAGE OF ACTIVITY**

TUKEY HSD MULTIPLE COMPARISONS.

MATRIX OF PAIRWISE COMPARISON PROBABILITIES:

REL.TIME	1	2	3	4	5	6	7	8	9	10
1	1.000									
2	0.000	1.000								
3	0.000	0.999	1.000							
4	0.000	0.997	1.000	1.000						
5	0.000	0.635	0.974	0.988	1.000					
6	0.000	0.945	1.000	1.000	1.000	1.000				
7	0.000	0.016	0.154	0.207	0.868	0.479	1.000			
8	0.000	0.000	0.006	0.010	0.226	0.046	0.991	1.000		
9	0.000	0.000	0.000	0.000	0.000	0.000	0.026	0.358	1.000	
10	0.000	1.000								

Metabolic rates of free-ranging platypuses

ACTIVITY LOGGER CALIBRATION:

REGRESSIONDEP VAR: **ACTIVITY** N: 1506 MULTIPLE R: 0.844 SQUARED MULTIPLE R: 0.713

ADJUSTED SQUARED MULTIPLE R: .713 STANDARD ERROR OF ESTIMATE: 56.843

<i>VARIABLE</i>	<i>COEF</i>	<i>STD ERROR</i>	<i>STD COEF</i>	<i>TOLERANCE</i>	<i>T</i>	<i>P (2 TAIL)</i>
CONSTANT	-32.327	5.279	0.000	.	-6.124	0.000
DIVE DURATION	9.898	0.162	0.844	1.000	61.144	0.000

ANALYSIS OF VARIANCE

<i>SOURCE</i>	<i>SUM-OF-SQUARES</i>	<i>DF</i>	<i>MEAN-SQUARE</i>	<i>F-RATIO</i>	<i>P</i>
REGRESSION	.120796E+08	1	.120796E+08	3738.570	0.000
RESIDUAL	4859534.474	1504	3231.073		

ANALYSIS OF VARIANCE

DEP VAR: **FMR MIN** (AL-DATA) N: 726 MULTIPLE R: 0.881 SQUARED MULTIPLE R: 0.776
 CATEGORICAL VALUES ENCOUNTERED DURING PROCESSING ARE:
 ANIMAL (24 LEVELS)

<i>SOURCE</i>	<i>SUM-OF-SQUARES</i>	<i>DF</i>	<i>MEAN-SQUARE</i>	<i>F-RATIO</i>	<i>P</i>
ANIMAL	.905428E+13	23	.377262E+12	101.057	0.000
SEASON	.793616E+13	3	.264539E+13	511.361	0.000
ERROR	.373507E+13	699	.517323E+10		

POST HOC TEST OF **FMR MIN** (AL-DATA)

TUKEY HSD MULTIPLE COMPARISONS.

MATRIX OF PAIRWISE COMPARISON PROBABILITIES:

SEASON	AUTUMN	SPRING	SUMMER	WINTER
AUTUMN	1.000			
SPRING	0.348	1.000		
SUMMER	0.000	0.000	1.000	
WINTER	0.000	0.000	0.000	1.000

ANALYSIS OF VARIANCE

DEP VAR: **FMR MIN** (TDR-DATA) N: 98 MULTIPLE R: 0.785 SQUARED MULTIPLE R: 0.616
 CATEGORICAL VALUES ENCOUNTERED DURING PROCESSING ARE:
 ANIMAL (11 LEVELS):

<i>SOURCE</i>	<i>SUM-OF-SQUARES</i>	<i>DF</i>	<i>MEAN-SQUARE</i>	<i>F-RATIO</i>	<i>P</i>
ANIMAL	.800679E+12	10	.800679E+11	36.882	0.000
SEASON	.609792E+12	1	.609792E+12	154.151	0.000
ERROR	.379758E+12	86	.395581E+10		

ANALYSIS OF VARIANCE

DEP VAR: **FMR MIN** N: 824 MULTIPLE R: 0.896 SQUARED MULTIPLE R: 0.802
 CATEGORICAL VALUES ENCOUNTERED DURING PROCESSING ARE:
 ANIMAL (29 LEVELS)?

<i>SOURCE</i>	<i>SUM-OF-SQUARES</i>	<i>DF</i>	<i>MEAN-SQUARE</i>	<i>F-RATIO</i>	<i>P</i>
ANIMAL	848554.570	32	26517.330	8.162	0.000
WATER TEMP	816444.428	1	816444.428	251.308	0.000
AIR TEMP	326.222	1	326.222	0.100	0.751
ERROR	2560038.132	789	3248.779		

ANALYSIS OF VARIANCE

DEP VAR: **FMR MIN** N: 824 MULTIPLE R: 0.940 SQUARED MULTIPLE R: 0.884
 CATEGORICAL VALUES ENCOUNTERED DURING PROCESSING ARE:
 ANIMAL (29 LEVELS)

<i>SOURCE</i>	<i>SUM-OF-SQUARES</i>	<i>DF</i>	<i>MEAN-SQUARE</i>	<i>F-RATIO</i>	<i>P</i>
ANIMAL	7.05983E+12	35	2.01710E+11	104.006	0.000
FORAGING DURATION	1.20111E+12	1	1.20111E+12	619.318	0.000
CLOUD COVER	4.30791E+10	1	4.30791E+10	22.213	0.000
RAINFALL	1.57948E+09	1	1.57948E+09	0.814	0.367
ERROR	1.47007E+12	785	1.93940E+09		

Appendix C: Technical supplier contact details

1. Time-depth recorder TDR_10

Lotek Wireless Inc.

114 Cabot Street, St. John's, Newfoundland, Canada A1C 1Z8

Internet: www.lotek.com

2. Activity logger Actiwatch

Mini Mitter Co., Inc.

20300 Empire Avenue Building B-3, Bend, Oregon 97701, USA

Internet: www.minimitter.com

3. Radio-transmitter

Faunatech, Ross Meggs

11, Wattle Grove, Eltham 3095 Victoria

ph: +61 3 9439 2165

4. Temperature logger

HOBO Thermocouple Logger & Stowaway Temperature Logger

Onset Computer Corporation

470 MacArthur Blvd, Bourne, MA 02532, USA

Internet: www.onsetcomp.com

5. Software MultiTrace 3.10

Jensen Software Systems

Lammertzweg 19, 24235 Laboe, Germany

e-mail: jlage.jss@t-online.de

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