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We investigated the activity patterns of platypuses, *Ornithorhynchus anatinus*, at Lake Lea, a subalpine lake in Tasmania. Platypuses were equipped with activity loggers or time–depth recorders, which allowed constant recordings for up to 48 days. The recordings revealed an unexpectedly high variety of foraging behaviors. Although nocturnal activity, as reported from other habitats, was still predominant, diurnal activity as well as highly fragmented activity patterns were common. Mean foraging duration was 12.4 h/day, with some animals foraging continuously for up to 29.8 h. Daily emergence and return times as well as durations of daily foraging trips varied considerably. At least 2 animals showed a distinct shift in activity pattern related to the lunar cycle. Season and water temperature affected platypus behavior. Foraging durations were longer and activity levels were higher in winter. In contrast to observations in river systems, temporal separation likely served as a mechanism to avoid intraspecific competition, and was particularly important for adult males during the breeding season. Dominant males were preferentially nocturnal, whereas lower-ranked males adopted more variable or fragmented activity patterns.

Key words: activity patterns, data-logger, foraging, lake system, *Ornithorhynchus anatinus*, platypus, Tasmania, temporal separation

The platypus, *Ornithorhynchus anatinus* (Shaw, 1799), is a semiaquatic mammal endemic to eastern Australia, including Tasmania. It can be described as an opportunistic carnivore (Faragher et al. 1979) and spends approximately one-half of the day foraging for benthic invertebrates, diving on average 75 times per hour with each dive lasting about 30 s (Bethge et al. 2003).

Foraging ecology and activity patterns of platypuses have been investigated in the past in a range of aquatic systems (Grant and Carrick 1978; Grant et al. 1992; Grigg et al. 1992; Gust and Handasyde 1995; Otley et al. 2000; Serena 1994). Radiotelemetry 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 has been observed during the breeding season as well as during winter, and spatial separation of individuals has been reported in a number of studies (Grant et al. 1992; Gust and Handasyde 1995; Otley et al. 2000; Serena

1994). In larger aquatic systems, platypuses show a decrease in home-range size and increased overlap of home ranges, a response shown by a number of mammals to increased population density (Sanderson 1966). This has been suggested to be typical for carnivorous semiaquatic mammals that occupy linear habitats (Gardner and Serena 1995).

The data reported in this paper form part of a broader study on the ecophysiology and energetics of platypuses in a subalpine lake system. Studies on platypus behavior in lake habitats are sparse. Most have been of populations occupying lowland river and stream systems on mainland Australia. Otley et al. (2000) investigated platypuses at Lake Lea (i.e., where this study was carried out) using radiotelemetry. Bethge et al. (2003) used time–depth recorders (TDRs) to investigate diving behavior and dive cycles of platypuses at the lake.

In this study, data-loggers measuring activity were used to elucidate activity patterns of platypuses. Because lakes have a lower proportion of shore relative to feeding areas compared with river systems, we predicted that activity patterns would be strongly influenced by the need to avoid competition and antagonistic encounters. High prey availability in a highly productive lake allows high population densities. At the same time, space for burrowing is limited. Consequently, spatial separation seems not to be a viable strategy for platypuses to avoid extensive home-range overlap. Instead, we predict that

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temporal separation between individuals is the main strategy to avoid intraspecific competition for food and mates.

MATERIALS AND METHODS

Field experiments were carried out at Lake Lea (41°30'S, 146°50'E), a subalpine lake in northwestern Tasmania. Platypuses were captured at 11 trapping sites located around the lake edge following the methods outlined in Grant and Carrick (1974) and Serena (1994). Suitable burrow areas were restricted to 1 consolidated steep earth bank of approximately 30 m in length at the lakeshore and about a dozen gently sloping earth banks at the lake and along the associated creeks. Unweighted and partially weighted gill nets were set in the lake and larger creeks and water bodies. Captured animals were processed following the methods outlined in Grant and Carrick (1978) and Bethge et al. (2003). Field methods met guidelines for animal care and use approved by the American Society of Mammalogists (Gannon et al. 2007).

Information on foraging behavior and activity patterns were obtained from 36 individual radiotracking sessions in 1998–2000, using 29 individual platypuses (17 adult males, mass = $2.10 \text{ kg} \pm 0.33 \text{ SD}$; 10 adult females, mass = $1.45 \pm 0.11 \text{ kg}$; 2 subadults [1 male and 1 female], mass = 1.26 kg and 1.71 kg , respectively). To gain insight into the population dynamics of the Lake Lea animals, social units were identified by analyzing data from the trapping sites in regard to sex as well as status of the animals. Twenty-three of the investigated individuals were assumed to be resident animals (i.e., ≥ 1 year between 1st and last capture), whereas 6 male individuals were assumed to be transient (i.e., < 1 year between 1st and last capture). Transient animals were assumed to enter and leave the lake through 1 of 5 small creeks that fed into or out of the lake. Sixty percent of animals were recaptured at the same site where they were trapped the 1st time. All other animals were recaptured at a different site.

Individuals were equipped with data-logger–transmitter packages (size: maximum $62 \times 28 \times 18 \text{ mm}$, mass: 50 g) as described in Bethge et al. (2003), consisting of a standard transmitter (Faunatech, Eltham, Victoria, Australia) and 1 of 2 types of data-loggers. Twenty-four individuals were equipped with activity loggers (ALs; Actiwatch; Mini Mitter Co., Inc., Bend, Oregon) measuring activity and light, whereas 11 platypuses were equipped with TDRs (LTD_10; Lotek Wireless Inc., St. John's, Newfoundland, Canada) that measured depth, ambient temperature, and light. Animals were released at the site of capture. After 2–6 weeks, the animals were relocated by radiotelemetry. They were recaptured and the devices were removed.

Activity loggers were square-shaped (size: $27 \times 26 \times 9 \text{ mm}$, mass: 17 g) and allowed recording of activity and, in some cases, light levels into a 32-kilobyte onboard memory chip. Activity in these devices was measured with an accelerometer, giving values that increase linearly with increasing activity. The devices were programmed to monitor activity in 2- and 5-min intervals. TDRs were of cylindrical

shape with a drop nose to decrease drag (length: 61.5 mm, diameter 18 mm, mass: 16 g). They were programmed to measure dive depth in 2-s intervals. At this setting, recordings of up to 11 days were possible. After retrieval of the devices, data were downloaded with specially designed readers and corresponding software (AL: RhythmWatch, Mini Mitter Co., Inc.; TDR: Tagtalk, Lotek Wireless Inc.) to a laptop computer.

A total of 824 foraging trips (11,045 h of foraging) were recorded, 726 using ALs and 98 using TDRs. Observations were made for periods between 5 and 48 days. The active period of platypuses was defined as the time span between onset and end of activity. Foraging duration measured by ALs was defined as the time span between the time of sharp increase in activity and the time of sharp decrease in activity. Foraging duration measured by TDRs was defined as the time span between the beginning of the 1st dive and the end of the last dive of each foraging trip. In 78 foraging trips, recorded light levels (indicating burrow exit and entry) were used to estimate beginning or end or both of the foraging activity more accurately. Mean times of sunrise and moonrise and sunset and moonset as well as water and air temperatures were calculated for each foraging trip, using standard charts as well as data from temperature loggers in and next to the lake, respectively.

Data were collected multiple times on the same individuals. 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 comparisons, the Tukey test was used. To test for differences between 2 means, standard *t*-tests were performed. A probability of 95% ($P < 0.05$) was accepted as indicating statistical significance. Data obtained from the 2 subadult animals and from different logger types were analyzed separately where appropriate.

RESULTS

The mean active period of platypuses at Lake Lea was $13.5 \text{ h/day} \pm 1.36 \text{ SD}$ ($n = 24$) and ranged from 3.4 to 30.8 h of continuous activity. Mean individual active periods ranged from 10.0 to 15.8 h/day. The beginning of each active period was characterized by low activity levels for an average of 0.8 h (range: 0–3.3 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 0.4 h (range: 0–2.5 h) was observed.

Foraging duration derived from the ALs was $12.4 \text{ h/day} \pm 1.14 \text{ SD}$ ($n = 24$). Individuals performed foraging trips of up to 29.8 h without resting. Foraging duration derived from the TDRs averaged $11.5 \pm 1.53 \text{ h/day}$ ($n = 11$) and ranged from 6.4 to 25.0 h of continuous foraging activity. Typically, all platypuses began foraging immediately after leaving the burrow and foraged continuously over the whole duration of the foraging trip.

Foraging duration measured both by TDRs and ALs was found to vary significantly according to season (ANOVA: AL: $F = 9.1$, *d.f.* = 1, 725, $P < 0.001$; TDR: $F = 4.3$, *d.f.* = 1, 97,

TABLE 1.—Mean seasonal foraging durations and active periods of platypuses (*Ornithorhynchus anatinus*) at Lake Lea, Tasmania, 1998–2000. TDR = time–depth recorder; AL = activity logger.

	Device	Spring	Summer	Autumn	Winter	Average
Foraging duration (h/day)	TDR		11.2		12.2	11.5
	AL	12.4	11.9	12.5	13.2	12.4
Active period (h/day)	AL	13.7	13.0	14.0	14.2	13.5

$P = 0.041$) but not according to the sex of the platypuses (ANOVA: AL: $F = 1.4$, $d.f. = 1$, 725, $P = 0.23$; TDR: $F = 1.5$, $d.f. = 1$, 97, $P = 0.23$). The same trends were observed for the active period (ANOVA: AL: season: $F = 9.1$, $d.f. = 1$, 725, $P < 0.001$; sex: $F = 0.2$, $d.f. = 1$, 725, $P = 0.65$). On average, animals were active about 1 h longer in winter than in summer. Results are summarized in Table 1.

Significant differences in activity levels among months were observed (ANOVA: $F = 18.5$, $d.f. = 1$, 725, $P < 0.001$). Daily activity was highest from August to November and lowest in January. Correspondingly, the degree of daily activity was significantly dependent on water temperature (ANOVA: $F = 16.2$, $d.f. = 1$, 725, $P < 0.001$). Lower water temperatures were associated with higher daily activity. The sex of the platypuses had no significant influence on the degree of daily activity (ANOVA: $F = 0.8$, $d.f. = 1$, 725, $P = 0.362$).

Data from both logger types were grouped into nocturnal, diurnal, and mixed activity patterns. A foraging trip was regarded as nocturnal if 80% of the trip was performed during nighttime (from 1800 to 0600 h). Accordingly, a foraging trip was regarded as diurnal if 80% of the trip was performed during daytime (from 0600 to 1800 h). All other trips were regarded as mixed.

Sixty-one percent of all foraging trips were nocturnal, whereas 31% were mixed and 8% were diurnal. Nocturnal activity was highest in summer and autumn, whereas diurnal activity occurred predominantly in the winter months (Fig. 1). Diurnal activity was mainly observed in female platypuses and

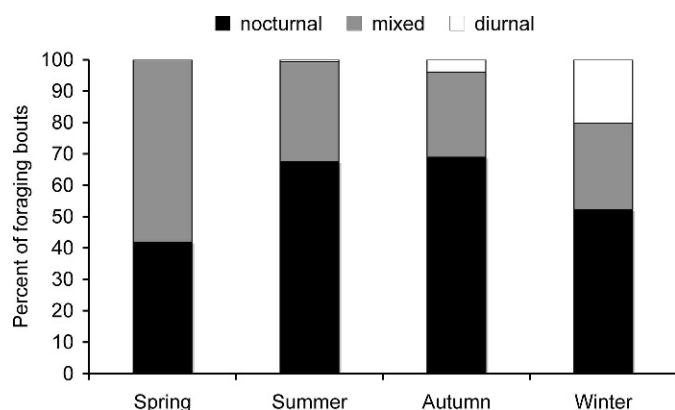


FIG. 1.—Percent of foraging trips classified in 3 activity patterns, separated by season, for platypuses (*Ornithorhynchus anatinus*) at Lake Lea, Tasmania, 1998–2000 (pooled data from 824 foraging trips of 29 individuals).

was rare in males. Females showed diurnal activity in 16% of all foraging trips, whereas males were diurnal in 2% of all trips. Strictly diurnal behavior over a number of consecutive days was only observed in winter in 3 adult females.

Platypuses showed a high variability in behavior (Fig. 2). Quite often, individuals changed start and end times of their active periods within days. Seemingly erratic changes in emergence and return times of up to a couple of hours as well as substantial changes in durations of foraging trips from day to day were obvious. Emergence and return times of the 2 subadults were much more regular than those of the adult platypuses. Both the subadult platypuses were strictly nocturnal.

Animals grouped into the activity pattern category mixed showed behavior that was even more erratic. In 3 animals, foraging activity was relatively regular but interrupted by very long foraging trips of up to 30.8 h. One platypus showed a distinct 24-h rhythm where 24-h foraging trips alternated with 24-h resting periods. Although only 7 days of activity were recorded, the animal still followed the same rhythm when it was recaptured 6 days later.

Two platypuses, a male and a female, clearly followed a lunar rhythm in their foraging patterns with both full and new moon possibly causing changes in behavior. Both animals synchronized their activity patterns with times of moonrise and moonset. At full or new moon, respectively, they slowly shifted their active period back by 1 lunar rhythm only to synchronize their behavior again with the moon at the next new and full moon, respectively (Fig. 3). Two more platypuses are likely to have been following lunar rhythms. However, observation periods in these animals were too short to confirm this suggestion.

Seven platypuses were equipped twice with data-loggers during this study, with a break between deployments of 6–21 months. Six of these 7 individuals showed the same activity pattern in both experiments. Only 1 female changed her activity pattern from diurnal (in winter) to nocturnal (in summer). Five of the 7 animals equipped twice were captured at the same sites both times they were captured.

DISCUSSION

Instrumental and experimental effects.—Effects of externally attached devices on swimming and diving animals range from increased duration of foraging trips, reduced swimming speeds, and reduced food intake to increased energy expenditure and impaired movements (Croll et al. 1991; Hull 1997; Wilson and Culik 1992; Wilson et al. 1986). However, the data-loggers used in this study did not cause a significant increase in the mean foraging metabolic rate of platypuses foraging in a swim tank (Bethge et al. 2001). This was most probably attributable to the streamlined shape of the devices, which was found to be important for minimizing instrument effect (Bannasch et al. 1994; Culik et al. 1994). The mass of the devices (50 g) only amounted to a maximum of 4.4% of body mass. Still, adverse effects of the devices on platypus foraging behavior cannot be ruled out and should be considered when interpreting the collected data.

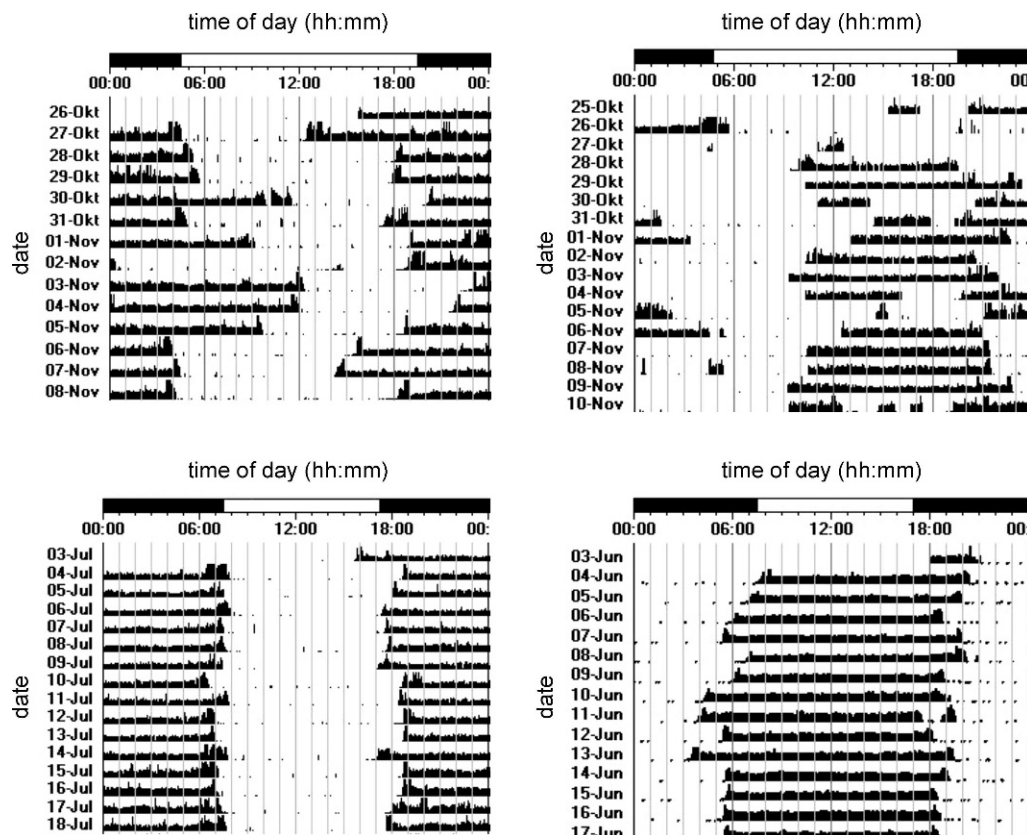


FIG. 2.—Sample activity records of 4 resident platypuses (*Ornithorhynchus anatinus*) at Lake Lea, Tasmania. Top: adult male (left) and female (right) in spring 1998; bottom: adult male (left) and female (right) in winter (1999 and 1998, respectively).

Activity patterns.—Nearly two-thirds of all platypuses examined at Lake Lea were mainly active during nighttime, confirming that platypuses are predominantly nocturnal, as reported in other studies (Grant et al. 1992; Grigg et al. 1992; Gust and Handasyde 1995; McLeod 1993; Serena 1994). However, highly variable activity patterns, including irregular as well as partly or strictly diurnal activity in more than one-third of all animals, were observed throughout the year. This suggests that activity patterns of platypuses are much more variable than previously reported, and that they are not solely influenced by the light–dark cycle but by a number of other ecological and physiological factors. For example, previous studies have noted that social organization, mating system, competition between individuals, abundance and dispersion of food, predator avoidance, or thermoregulation costs are likely to influence activity patterns of platypuses in the wild (Francis et al. 1999; Gardner and Serena 1995; Grant et al. 1992; Gust and Handasyde 1995; Otley et al. 2000; Serena 1994).

The effects of temperature on the activity of platypuses have been an issue of great debate in the past. Some early researchers questioned the ability of the platypus to forage in cold water for long periods (Burrell 1927; Smyth 1973). Today, it is widely accepted that the thermoregulatory mechanisms of the animal are excellent (Grant and Dawson 1978a, 1978b). However, reports on the duration of active periods in platypuses differ enormously and range from 7 to 19 h/day depending on habitat (Table 2). Records from

Badger Creek (Serena 1994) and the Goulbourn River (Gust and Handasyde 1995), Victoria, as well as the Shoalhaven River, New South Wales (Grant 1983), are slightly shorter than records from the Thredbo River, New South Wales (Grant et al. 1992), and Lake Lea in Tasmania (this study; Otley et al. 2000), where in the winter months water temperatures frequently approach 0°C.

It seems likely that in cold habitats platypuses forage for longer periods because there is an increased energy cost of thermoregulation, combined with a reduction in availability of food, because size and diversity of benthic organisms are likely reduced over the winter months (Faragher et al. 1979; Lamm 1993). This will reduce the energy return to the platypus on each dive. In response to this, platypuses at Lake Lea foraged approximately 1 h longer in winter than in summer (Table 1).

As another response to increased energy costs in the cold season, Grant (1983) suggested a shift to diurnal activity in winter, avoiding times of lowest air temperatures. Gust and Handasyde (1995) observed a higher incidence of diurnal activity of platypuses in late winter in the Goulbourn River, Victoria. Consistent with this, platypuses at Lake Lea switched to more diurnal activity during winter (Fig. 1). However, the energy savings of diurnal activity will be quite small. Water temperature, which was very stable during winter, is much more important for the energy budget of platypuses than is air temperature. Most of the time when out of the burrow, platypuses are in water. Minimum conductance in water is

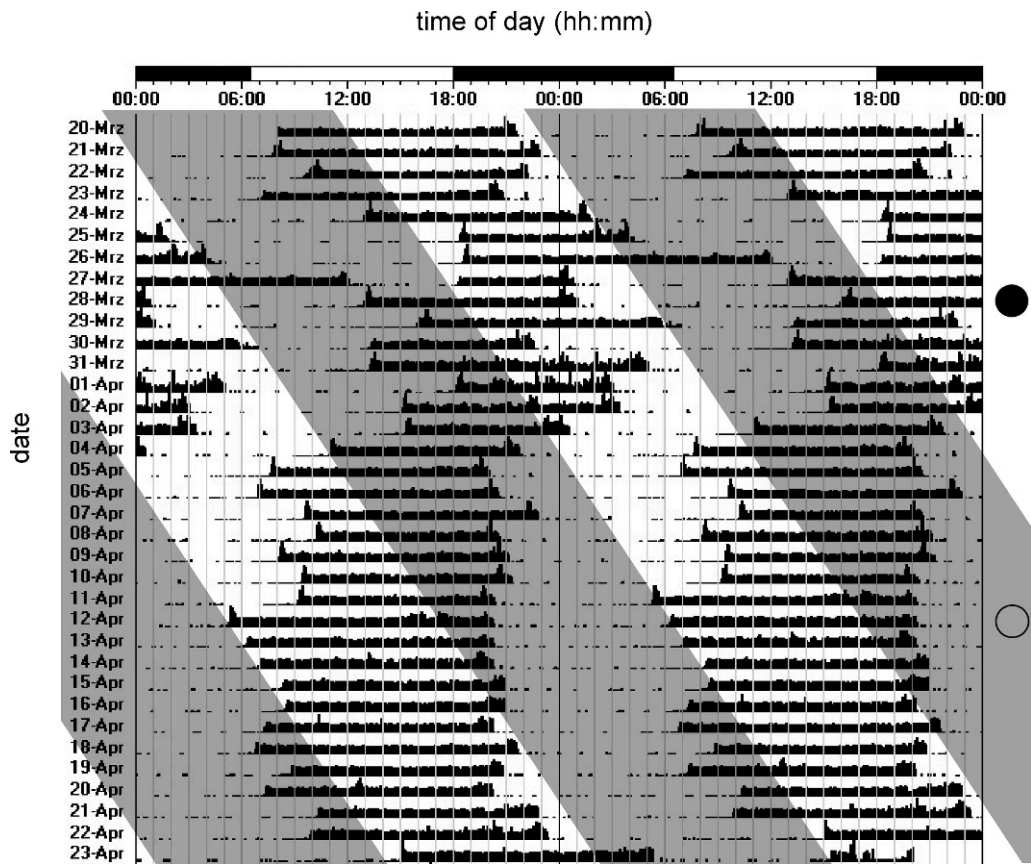


FIG. 3.—Sample actogram of a male platypus (*Ornithorhynchus anatinus*) at Lake Lea, Tasmania, showing a lunar activity rhythm. Shaded areas show moonlight hours. Circles show new (closed circle) and full (open circle) moon.

about 2.4 times minimum conductance in air (Grant and Dawson 1978b). A drop in air temperature from 5°C to −5°C would increase metabolic rate in air by 30–40%. But this metabolic rate would still be only about one-half of that in water at 5°C (calculated from Grant and Dawson [1978b]). More evidence that diurnal activity does not have a profound effect on platypus energy budgets is the observation that subadult animals, despite their small body size, were all strictly nocturnal.

Although the platypus is considered to be essentially a solitary species, in some studies social units have been identified (Grant 1992; Grant et al. 1992), consisting of resident as well as transient individuals. The latter were found to be predominantly male and possibly represented dispersing

TABLE 2.—Comparison of active periods recorded for platypuses (*Ornithorhynchus anatinus*).

Active period (h/day)	Habitat	Source
9.6–12.2	Shoalhaven River, New South Wales	Grant (1983)
8.9–18.8 ^a	Thredbo River, New South Wales	Grant et al. (1992)
7.3–12.4 ^a	Badger Creek, Victoria	Serena (1994)
9.8–10.5	Goulbourn River, Victoria	Gust and Handasyde (1995)
8.5–16	Lake Lea, Tasmania	Otley et al. (2000)
10.0–15.8	Lake Lea, Tasmania	This study

^a Derived from burrow times.

subadults (Grant 1992) ready to take up vacant sites or occupy home ranges from resident males (Gardner and Serena 1995). Spatial separation due to social interactions also has been observed. Radiotracking studies by Serena (1994) in Victoria showed that adult males did not tolerate other adult males, an observation also made by Gardner and Serena (1995). In contrast, adult females are not territorial in the sense of defending mutually exclusive areas and tolerate a great deal of spatial overlap between individuals (Serena 1994).

The degree of social tolerance varied between habitats. In narrow lotic habitats, male platypuses engage in territorial defence. Population densities of only 1 or 2 individuals per kilometer of waterway are the consequence (Gardner and Serena 1995; Serena 1994). In contrast, broader habitats and weir systems, where prey availability is higher, show much higher population densities (Grant and Carrick 1978). In the latter habitats, a point may be reached where area defense is not a viable strategy (Brown and Orians 1970). Consequently, platypuses tolerate more home-range overlap (Gust and Handasyde 1995; McLeod 1993).

Given these results, what would one expect in a lake system? Otley et al. (2000) pointed out that, in lake systems, although there is a much larger foraging area in a lake, there is not a proportional increase in bank area available, resulting in the need to share a limited number of suitable burrow sites. This is a profound difference to river systems where availability of burrow sites normally is not a limiting factor.

Consequently, with abundant prey in a highly productive lake, limited burrow sites have to be shared by many individuals.

Indeed, in this study, platypuses showed a high tolerance for sharing burrow areas. Up to 6 resident females were caught in the vicinity of 1 particular burrow area. On 12 occasions, >1 resident male (up to 3) shared the same burrow area, resulting in profound intraspecific competition. As a consequence, platypuses showed substantial temporal separation. Although females followed a variety of activity patterns seemingly not related to their social status, analysis of data from 3 closely monitored trapping sites suggests that dominant males were predominantly nocturnal. Other males—some resident, some transient—showed mixed activity patterns. The prevalence of nocturnal activity by the dominant males was most pronounced during the mating season.

Cloudsley-Thompson (1980) reported a strategy of temporal separation in a variety of animals. Temporal separation has been postulated to contribute to improved foraging efficiency and to develop as an outcome of aggressive behavior serving primarily to deter immigration by nonneighbors (Cloudsley-Thompson 1965; Gardner and Serena 1995). At Lake Lea, daily rhythms of platypuses shifted on average to more irregular activity pattern in spring when the highest percentage of transient males was present in the lake. During this time, >50% of all animals showed mixed behavior (Figs. 1 and 2). Irregular activity patterns could relate to an increase in searching behavior for mates and, accordingly, an increase in competition among male platypuses. Gust and Handasyde (1995) reported some temporal separation between adult males during the breeding season and found greater variation in the times at which animals emerged from their burrows. Grant (2007) also noted that males are highly engaged in courtship as well as in defending their territory against competitors in spring.

Lower-ranked animals might choose to avoid emergence and return times of dominant individuals living at the same burrow site. This might include the observed strategy of temporarily following the lunar rhythm, which has not been reported in platypuses before (Fig. 3). Moonlight clearly provides platypuses with a visual clue, which can be easily used to synchronize foraging activity. Following this distinct pattern could temporally separate the peak foraging activity of the platypuses in question from that of strictly nocturnal or strictly diurnal animals, thus reducing intraspecific competition. However, following the lunar rhythm also might be prey related. Such behavior is observed in animals that live close to the ocean and feed in intertidal areas (Refinetti 2000; Wikelski and Hau 1995). Still, whether the prey of platypuses at Lake Lea, such as the endemic burrowing crayfish *Parastacoides tasmanicus tasmanicus* (Munks et al. 2000), follows a lunar rhythm remains unknown.

Hawkins (1998) found temporal separation in captive platypuses and reported that the activity of the subordinate animal moved more into the high-light periods, and became more fragmented and shortened when a dominant animal was present. This is consistent with the highly irregular activity recorded in platypuses at Lake Lea, especially during the breeding season when dominance behavior is probably at a peak. Interestingly,

activity patterns of individuals did not change much over time during this study. Six of the 7 platypuses that were equipped twice with data-loggers showed the same activity pattern in both monitoring periods. This suggests that the animals occupy a relatively stable social position in the overall population.

The 2 juvenile platypuses investigated in this study followed very strict nocturnal rhythms. Home ranges of juvenile as well as subadult platypuses 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.

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