The life history of an egg-laying mammal, the echidna (*Tachyglossus aculeatus*)[1]

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Abstract: Echidnas have a low metabolic rate, and energy expenditure is reduced even further by the use of torpor and hibernation. Thus, echidnas appear to lie at the slow extreme of the fast–slow continuum, and this is reflected in many aspects of echidna life history: a long life, a long lactation period, and a single young that matures late. Reproductive activity occurs in mid-winter, shortly after arousal from hibernation. After a pregnancy of about 3 weeks the female lays a single egg into her pouch that hatches after 10–11 d. Initially, the young is incubated in the pouch. Later, it is left in the nursery burrow while the mother forages for ants, termites, and other invertebrates. Lactation lasts for 150–200 d, the duration differing significantly between geographic regions. Growth rates during late lactation are very high, and, when weaned, the young has reached about 40% of adult mass. The young loses mass before entering its first hibernation, which extends from early autumn to late spring. The young echidna reaches adult mass after about 3–5 years.
Keywords: echidna, egg-laying, growth, hibernation, life history, metabolic rate, monotreme.

Résumé : Les échidnés ont un métabolisme lent et leurs dépenses énergétiques sont réduites d'autant plus par la torpeur et l'hibernation. Ainsi les échidnés semblent se situer à l'extrémité lente du continuum rapide-lent et cela se reflète dans plusieurs aspects de leur histoire de vie : une longue durée de vie, une longue période de lactation, un seul jeune qui atteint la maturité tardivement. L'activité reproductive arrive au milieu de l'hiver, peu de temps après le réveil de l'hibernation. Après une grossesse d'environ 3 semaines, la femelle pond dans sa poche un œuf unique qui éclot après 10-11 jours. Au début, le jeune est incubé dans la poche, ensuite il est laissé dans un terrier pouponnière pendant que la mère cherche des araignées, des termites et d'autres invertébrés. La lactation dure 150–200 jours, la durée variant de façon significative entre les régions. Les taux de croissance sont très élevés à la fin de la lactation et lorsque le jeune est sevré, il a atteint environ 40 % de la masse adulte. Le jeune perd de la masse avant d'entrer dans sa première hibernation qui dure du début de l'automne jusqu'à tard au printemps. Le jeune échidné atteint la masse adulte après 3–5 ans.
Mots-clés : croissance, échidné, hibernation, histoire de vie, métabolisme, monotrème, ponte d'œufs.

Nomenclature: Griffiths, 1989.

Introduction

Egg-laying differentiates the life histories of the monotremes dramatically from those of other mammals. Of the extant monotremes, there is very little information on the life histories of the 3 known species of the genus *Zaglossus*, which are confined to New Guinea (Flannery & Groves, 1998). Aspects of the life history of the platypus (*Ornithorhynchus anatinus*) have been subject of a number of studies (Hulbert & Grant, 1983; Grigg *et al.,* 1992; Jabukowski *et al.,* 1998; Bethge, Munks & Nicol, 2001; Bethge *et al.,* 2003), some of which have extended over sufficiently long periods to allow reasonable estimates of parameters such as longevity, breeding success, and recruitment (Grant, 2004; Grant, Griffiths & Temple-Smith, 2004).

The short-beaked echidna, *Tachyglossus aculeatus*, although restricted to Australia and New Guinea, is the most widely distributed of the extant monotremes. In New Guinea, echidnas occur in both coastal and highland areas (Van Deusen & George, 1969). In Australia, echidnas are nearly ubiquitous in their distribution, occupying a diverse range of habitats from mild coastal areas to above the snow-line (Griffiths, 1968; Grigg, Beard & Augee, 1989). Despite this huge geographic range and diversity of habitats, all short-beaked echidnas are assigned to the same species, which is divided into five geographic subspecies (Griffiths, 1978). Reviews of echidna biology have usually assumed that life histories of echidnas from different areas or subspecies are essentially identical (Jackson, 2003), but in fact some key life history parameters differ between geographic populations or subspecies (Nicol & Andersen, 2006).

This review will concentrate on material gathered during our field studies in Tasmania but will also refer to and highlight differences between subspecies.

METABOLIC RATE

Table I summarizes metabolic rate data for echidnas. Excluding the data point from Schmidt-Nielsen, Dawson, and Crawford (1966), which is considerably higher than other measurements and for which no measure of variability is given, the mean value for basal metabolic rate (BMR) is 0.15 ± 0.01 mL $O_2 \cdot g^{-1} \cdot h^{-1}$, 33% of the value predicted for mammals by the Kleiber equation (Kleiber, 1932) and one of the lowest observed in mammals (Dawson, Grant & Fanning, 1979; McNab, 1984). Echidnas also have a low body temperature (T_b). When not hibernating or torpid,

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T_b ranges from 28 to 35 °C, with a modal T_b of 31–32 °C (Nicol & Andersen, in press). The low T_b and metabolic rate of echidnas have been attributed variously to their phylogenetic status (Martin, 1902; Dawson, Grant & Fanning, 1979), their diet (McNab, 1984), and geographic factors, including climatic variability (Lovegrove, 2000). While it is difficult to untangle correlation and causality, the echidna shows a suite of ecological and life history variables that have been correlated with a low BMR. Echidnas eat ants, termites, and other soil invertebrates (Smith, Wellham & Green, 1989; Griffiths *et al.,* 1990; Abensperg-Traun, 1994), and low T_b and low BMR have been correlated with ant and termite eating in mammals over 1 kg (McNab, 1984). Interestingly, there are no marsupial counterparts of the echidna, presumably because the ant-eating niche was already occupied by the echidna in Australia. The nearest ecological equivalent is the numbat (*Myrmecobius fasciatus*), with a mass of about 500 g, which feeds exclusively on termites, but is at risk of extinction. The numbat also has a low T_b and BMR, but these are well within the range of values seen in other marsupials (Cooper & Withers, 2002). The echidna is also semi-fossorial: the mother raises the single young in a nursery burrow, and during hibernation echidnas will often cover themselves with soil; in mammals a fossorial habit is associated with low BMR (McNab, 1979). Echidnas are protected by a dense covering of spines, and armoured and spiny mammals also have low metabolic rates (Lovegrove, 2001).

BMR is generally believed to be an indicator of metabolic capacity (Frappell & Butler, 2004; Ksiazek, Konarzewski & Lapo, 2004), and the BMR of mammals correlates with many life history variables (White & Seymour, 2004). Although there has been debate about how the metabolic constraints on life history variables relate to BMR (Harvey, Pagel & Rees, 1991; Johnson, Thomson & Speakman, 2001; Mueller & Diamond, 2001), in eutherian mammals energy expenditure on reproduction is positively correlated with energy expended on maintenance, such that high-maintenance species harvest more energy and expend more on reproduction than low-maintenance species (McNab, 2002), while a low BMR optimizes longevity. The low metabolic rate of the echidna is reflected in many aspects of its life history: it has a long life, a long lactation period, and produces a single young that matures late.

Although there is an overall significant correlation between BMR and field metabolic rate (FMR) in mammals (White & Seymour, 2004), analysis is complicated by the fact that FMR and BMR scale differently against body mass (Nagy, 2005). Generally, in small mammals the ratio of FMR:BMR varies from 1.6 to 7.6, with an average value of 3.4 (Speakman, 2000). There have been 2 studies of field metabolic rates (FMR) in echidnas (Green, Griffiths & Newgrain, 1992; Schmid *et al.,* 2003), and these found rates 3–4 times greater than BMR. Table II compares metabolic and life history parameters for the echidna, a eutherian hibernator of comparable mass, the yellow-bellied marmot (*Marmota flaviventris*), and the other common monotreme, the platypus (*Ornithorhynchus anatinus*). There are no comparable marsupial hibernators: the only marsupials to show prolonged hibernation, as distinct from daily torpor, weigh less than 100 g (Geiser, 1994). The FMR:BMR of *Marmota flaviventris* reflects the fact that the FMR value is comparable to other rodents and 135% of that predicted for mammals generally, while the BMR value is relatively low. The high FMR:BMR of the platypus reflects the energetic costs of foraging in cold water (Bethge, Munks & Nicol, 2001). By contrast, the FMR of echidnas is 40–50% of that predicted for mammals (Nagy, Girard & Brown, 1999), *i.e.,* BMR and FMR are comparably low.

During hibernation, the metabolic rate of echidnas is comparable to that of other hibernating mammals (Nicol, Andersen & Mesch, 1992; Nicol & Andersen, 1993). As noted by Geiser (1988), hibernators at low T_b represent the only example in which mass-specific metabolism does not increase exponentially with decreasing body mass. This means that the energy savings for large hibernators are much less than for small hibernators (Singer & Bretschneider, 1990). Several aspects of the biology of the echidna suggest that the energy benefit of hibernation would be modest, particularly given the energy cost of periodic arousals (Nicol & Andersen, 1993): the very low FMR reduces the energy saved by hibernating, and because reproductively active echidnas arouse before the coldest part of the year, they do not avoid the costs of thermoregulation. Despite this, all populations of echidnas studied throughout Australia show some degree of torpor or hibernation (Nicol & Andersen, 1996).

HIBERNATION IN THE ANNUAL CYCLE OF THE ECHIDNA

In Tasmania all echidnas appear to hibernate (Nicol & Andersen, 2002). Using implanted temperature loggers, we have been able to obtain detailed records of timing of 13 adult echidnas (4 male, 9 female), with up to 8 y of recording from an individual echidna. Adult male echidnas

TABLE I. Compilation of metabolic rate data for echidnas. BMR: basal metabolic rate, FMR: field metabolic rate.

	Reference	Mass (kg)	mL $O_2 \cdot g^{-1} \cdot h^{-1}$	kJ·kg^{-1}·d^{-1}
BMR	(Martin, 1902)	2.36	0.151 ± 0.028	72.8 ± 13.5
BMR	(Schmidt-Nielsen, Dawson & Crawford, 1966)	3	0.217	104.6
BMR	(Dawson, Grant & Fanning, 1979)	3.4	0.132 ± 0.006	63.7 ± 2.9
BMR	(McNab, 1984)	3.58	0.153 ± 0.017	73.8 ± 8.4
BMR*	(Bech, Nicol & Andersen, 1992)	2.73	0.174 ± 0.029	83.9 ± 14.0
BMR	(Frappell, Franklin & Grigg, 1994)	3.12	0.155 ± 0.031	75.0 ± 14.8
FMR	(Green, Griffiths & Newgrain, 1992)	2.86	0.634 ± 0.06	306 ± 29
FMR	(Schmid *et al.*, 2003)	3.35	0.472 ± 0.06	228 ± 29
Hibernating	(Nicol & Andersen, 1993)	2.2	0.022	10.6

*Animals had access to food.

TABLE II. A comparison of life history data of the echidna with the yellow-bellied marmot, a eutherian hibernator of comparable mass, and the platypus, another monotreme.

	Echidna (*Tachyglossus aculeatus*)	Marmot (*Marmota flaviventris*)	Platypus (*Ornithorhynchus anatinus*)
Adult mass (kg)	2–7	2–5	0.9–2.5
Time to reach adult mass (y)	4–6	2	1
No. of young	1	5	1–2
Hatching/birth mass (g)	0.3	30	0.3
Age at weaning (d)	150* 200–210†	35	150
Mass at weaning (kg)	0.7–2.1	0.3–0.4	0.9
% adult mass	28–48%	≈10%	56–67%
Maximum growth rate of an individual (g·d^{-1})	40 (pre-weaning)	30 (post-weaning)	
BMR (kJ·kg^{-1}·d^{-1})	84	108	178
FMR (kJ·kg^{-1}·d^{-1})	240	763	1033
FMR:BMR	3	7	6
Life span (y)	50?	7	Male 7 Female 10–16

Marmot data from Leniham and van Vuren (1996), Nowack (1999), and Woods and Armitage (2003); platypus data from Dawson, Grant, and Fanning (1979), Munks *et al.* (2000), Bethge, Munks, and Nicol (2001), Holland and Jackson (2002), and Grant (2004).

* Tasmania; † Kangaroo Island and Western Australia.

hibernated from February 12 ± 10 (mean ± SD, *n* = 6) to July 2 ± 38 (*n* = 8), adult females in reproductive years from March 11 ± 10 (*n* = 9) to July 25 ± 21 (*n* = 13), and adult females in non-reproductive years from March 13 ± 21 (*n* = 13) to September 21 ± 16 (*n* = 19). It is important to note that these data are based on the 13 echidnas with data loggers, which allow the precise timing of hibernation events. Time of entry into hibernation is difficult to determine from field observations, as echidnas may reduce their activity well before T_b falls, whereas observing an active animal is an unambiguous indication that it is not hibernating. Even then, as echidnas often move to another location during their periodic arousals, observing an active echidna does not mean that it has finished hibernating for that year. We have, however, observed several females active and mating in early June, 2 weeks before the earliest date recorded from any of the females with a data logger. Figure 1 shows 3 consecutive years of T_b data from a female echidna, and Figure 2 summarizes all data on entry into hibernation and emergence obtained from data loggers. These figures illustrate the very early entry into hibernation and the difference in the length of hibernation for females in breeding and non-breeding years. The earliest entry and arousal we have recorded were from a male that began hibernation on January 30 and finished on May 16. As can be seen from
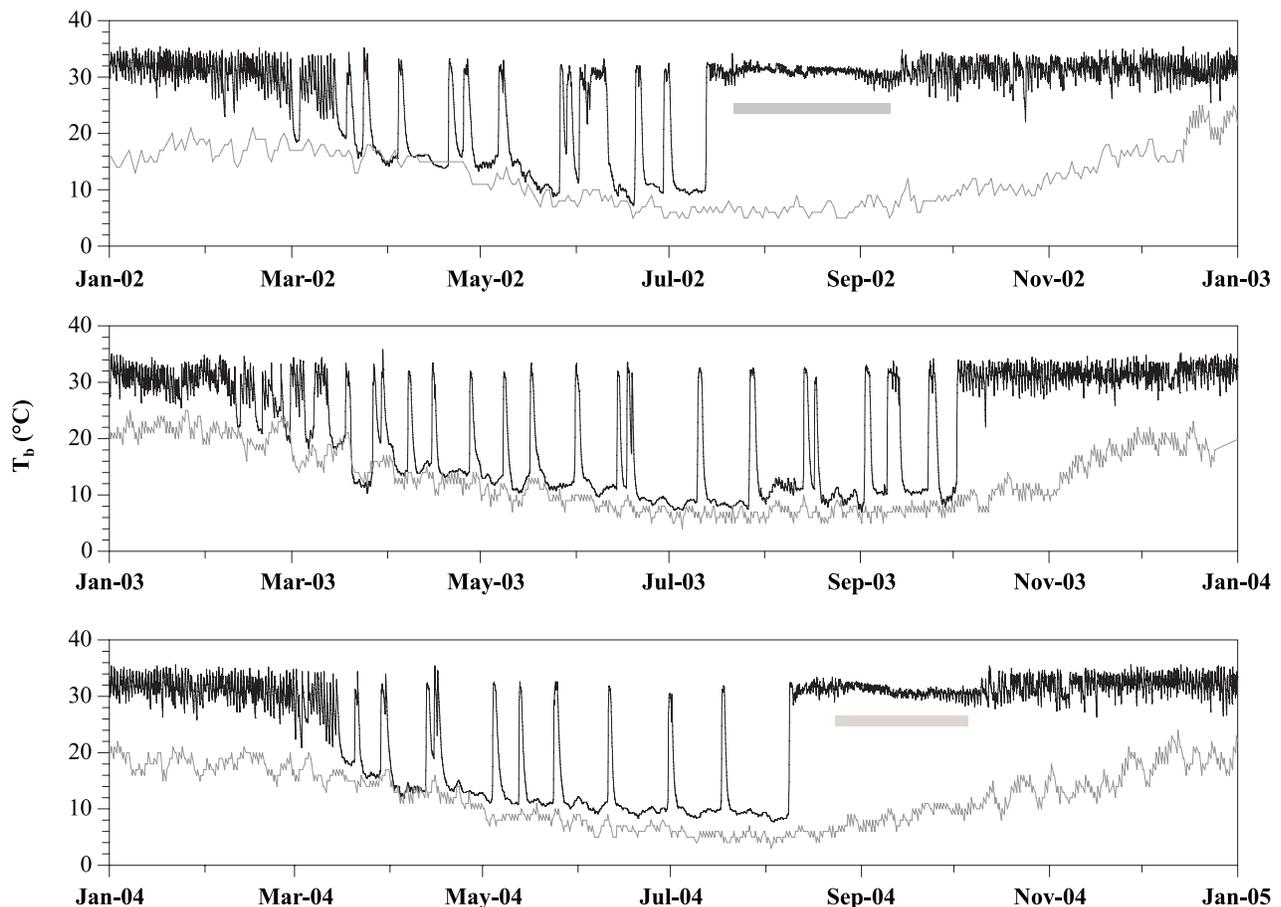

FIGURE 1. Body temperature (T_b) over 3 consecutive years for an adult female echidna. The grey line shows soil temperature in the study area within a few km of the echidna. Grey bars indicate the period of low T_b variability when the mother was in a nursery burrow in 2002 and 2004. "Test drops"—significant but short falls in T_b before entry into hibernation proper—are particularly obvious during 2002 and 2003.
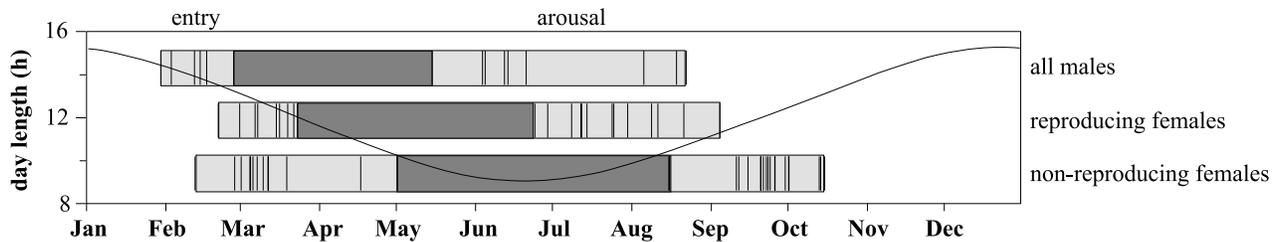
FIGURE 2. Summary of the timing of entry and emergence from hibernation for 13 adult echidnas in Tasmania determined from body temperature measured by implanted data loggers. Individual dates are shown by vertical lines. Shading extends from the first entry into hibernation until the last arousal, and the dark shading indicates the period from the last entry into hibernation until the first arousal. Solid curve is day length. Revised from Nicol, Vedel-Smith and Andersen (2004).

Figure 2, the majority of entries are between the summer solstice and the autumn equinox. In other studies from eastern Australia, the timing of hibernation is similar, with the length of the hibernation season decreasing in more northerly populations. At Mount Kosciusko in southeast Australia (36° S) the timing of hibernation is very similar to Tasmania (42° S), with the first observed entries on February 3 and the last arousals on October 21 (Beard, Grigg & Augee, 1992; Grigg, Augee & Beard, 1992). At New England in northern New South Wales (30° S) hibernation has been observed from April 2 until September 29 (F. Falkenstein, G. Körtner & F. Geiser, unpubl. data), and at Texas, Queensland (28° S), hibernation has been recorded from May 1 until August 17 (Beard & Grigg, 2000). However, on Kangaroo Island, South Australia (36° S), where the subspecies is *T. a. multiaculeatus*, "a very distinctive echidna" (Griffiths, 1989), Rismiller and McKelvey (1996) recorded brief periods of torpor between June 8 and August 17, although Green, Griffiths, and Newgrain (1992) noted torpor in Kangaroo Island echidnas in April and May and measured extremely low rates of water influx during these months.

Maximal mass gain occurs in late spring–early summer (see below). At the end of this period echidnas progressively reduce their activity and food intake, and T_b records may show evidence of test-drops before entry into hibernation proper (Figure 1). Echidnas appear to follow this pattern over all of their range, suggesting it is not simply a response to local food availability. In most parts of Tasmania food is available throughout the year, and Figure 2 shows that at any time of the year except perhaps for a short period in May, some Tasmanian echidnas will not be hibernating. For females it seems likely that the timing of hibernation reflects a balance between a drive to maximize energy savings by hibernating for as long as possible and mating at a time that will maximize the chances of survival of the young in the following hibernation season, rather than simply being a response to a shortage of food. A female arousing from hibernation in late July and mating within a few days would wean her young in early January (see section on growth rates and lactation), about 8 weeks before the overall mean time for entry into hibernation. For males the trade-off is likely to be between maximizing energy savings by hibernating and being ready to mate with females when they arouse from hibernation (Nicol & Andersen, 1993; Nicol & Andersen, 1996; Nicol & Andersen, 2002). From our field observations, juvenile echidnas in their first year appear to enter hibernation at about the same time as females that have been lactating, and juvenile echidnas in their first or second year do not emerge from hibernation until October–November.

REPRODUCTIVE ACTIVITY

Echidna populations from a range of latitudes and belonging to different subspecies show remarkably little variation in the timing of mating. In Tasmania mating occurs from early June to mid-September (Nicol & Andersen, 2006), whereas in the much colder Mount Kosciusko area the mating season begins a few weeks later and extends from early July to early September (Beard, Grigg & Augee, 1992), and on milder Kangaroo Island some mating activity has been reported as early as May (Rismiller & Seymour, 1991). On Kangaroo Island there is a courtship period of several weeks when a female may be pursued by a number of males ("echidna trains", Rismiller & McKelvey, 2000), but in Tasmania the majority of matings occur within one or 2 d of arousal from hibernation (Nicol, Andersen & Jones, 2005; Nicol & Andersen, 2006). Towards the end of the gestation period of 23 ± 1 d (Rismiller & McKelvey, 2000), in eastern Australian populations the mother enters a nursery burrow (Beard, Grigg & Augee, 1992; Beard & Grigg, 2000; Andersen & Nicol, 2004), and the egg is laid into the pouch, where it is incubated for 10–11 d before hatching (Griffiths, McIntosh & Coles, 1969). On Kangaroo Island the female forages with the egg and then the young in the pouch and deposits the young in a nursery burrow at 45–55 d (Rismiller & McKelvey, 2000). The mother then returns every 5–10 d to feed it (Griffiths *et al.,* 1988). In Tasmania, the mother does not normally leave the nursery burrow until the young is 25–35 d old (Nicol & Andersen, 2006), after which she will leave it alone in the nursery burrow, typically for 3–5 d in this early period, while she forages. Other echidna populations or subspecies have maternal strategies between these extremes.

ADULT MASS

The size of a mammal is the major determinant of many aspects of its life history (Eisenberg, 1981; Woodward *et al.,* 2005). Allometric relationships exist between body size and many variables, such as energy turnover, brain mass, life span, growth rates, and home range (Calder, 1983). Body size also constrains diet and habitat use (McNab, 2002). A major focus of many studies is the departure of physiological or life history variables from their allometrically predicted values (Dawson, Grant & Fanning, 1979; Lovegrove,

2000; McNab, 2002). Differences in sizes between sexes are also important, as these correlate with mating systems (Eisenberg, 1981).

Adult echidnas range in body mass from 2 to 7 kg, but there is some evidence of differences in body mass of echidnas from different populations or subspecies. A comparison of masses of adult echidnas from our study area showed males to be significantly heavier than females (males 4.1 ± 0.3 kg, $n = 13$, maximum 5.7 kg; females 3.8 ± 0.4, $n = 15$, maximum = 5.5 kg; $t = 2.92$, $P = 0.007$; based on an average of 10 observations per animal over a period of 38 months). In a study in southeast Queensland, adult males were also found to be heavier than females (4.1 ± 0.5 kg, $n = 10$ *versus* 3.4 ± 0.6 kg, $n = 9$; Beard & Grigg, 2000). By contrast, on Kangaroo Island mean body mass at the beginning of the courtship period for females was 3.7 ± 0.5 kg ($n = 6$) and for males 3.0 ± 0.2 kg ($n = 7$), with this difference being significant (Rismiller & McKelvey, 2003). The highest body masses recorded are from a study in the Snowy Mountains, where reproductively active females ranged from 3.9 to 7.0 kg (Beard, Grigg & Augee, 1992).

ANNUAL VARIATION IN BODY MASS

In all populations that have been observed, echidnas show significant annual variation in mass (Green, Griffiths & Newgrain, 1992; Beard & Grigg, 2000; Rismiller & McKelvey, 2000; Rismiller & McKelvey, 2003). At our southern Tasmanian midlands study area, adult males show a seasonal variation in body mass of about $\pm 25\%$, and females of about $\pm 30\%$. These mass changes are associated with the annual cycle of torpor or hibernation and reproductive activity, and reflect the large changes in energy balance. We have obtained 2 consecutive mass records from individual hibernating echidnas on 5 occasions (time between weighings 77–224 d), with an average loss of mass of 3.5 ± 0.9 g·d^{-1}, similar to the 4 g·d^{-1} reported by Hill and Florant (2000) for *Marmota flaviventris*. Assuming an average metabolic rate for hibernating echidnas of 0.022 mL·g^{-1}·h^{-1} (Nicol & Andersen, 1993), which equates to 42 kJ·d^{-1} for a 4 kg animal, this could be supported by the catabolism of 1.1 g fat·d^{-1}, compared with the 3.5 g·d^{-1} of mass actually lost, suggesting the main energy cost during hibernation is associated with arousals and the activity during those arousals. In *Marmota monax* euthermic arousals account for approximately 70% of the mass lost during hibernation (Zervanos & Salsbury, 2003).

Over the approximately 130 d of hibernation of the average reproductively active male or female echidna (Nicol & Andersen, 2002), these rates of mass loss would result in a total loss of about 460 ± 118 g. By contrast, females confined to the nursery burrow while they were incubating an egg and then the pouch young lost 16 ± 8 g·d^{-1} ($n = 6$), 4 times the rate of mass loss during hibernation, giving a loss of mass of about 480 ± 240 g over 30 d. Similarly, males during mating activity lost 14 ± 7 g·d^{-1} ($n = 7$), which would produce a mass loss of about 840 ± 420 g over 60 d.

Figure 3a (females) and b (males) shows the body mass data from all reproductively active echidnas, redrawn onto a single 18-month period. Superimposed on these are mass changes calculated from a simple model based on the
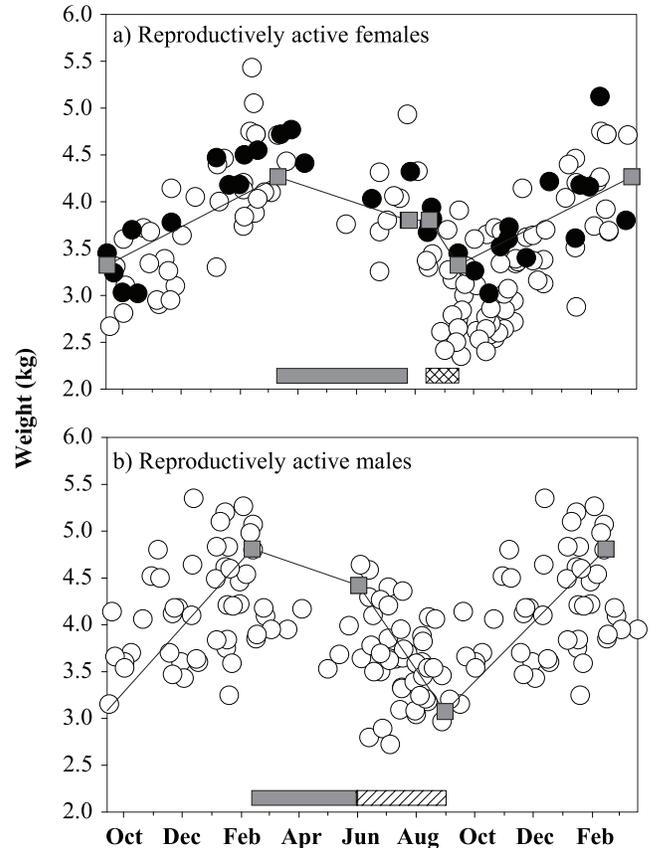

FIGURE 3. Annual body mass changes in reproductively active echidnas. a) Reproductively active females (open circles), *i.e.,* females which had young in the breeding season shown, redrawn onto a single 18-month period. Filled circles: echidna (animal id: 5D5E). Squares and lines show a simple model of annual mass change calculated assuming entry into hibernation on March 11 and arousal on July 25, with a mass loss during hibernation of 3.5 g·d^{-1}. Mating is assumed to occur 1 d after arousal, with entry into the nursery burrow 21 d after mating. The model assumes that between arousal and entry into the nursery burrow the female does not change in mass, but when in the nursery burrow she loses 16 g·d^{-1}. Grey horizontal bar: hibernation period; cross-hatched bar: period when the female is confined to the nursery burrow. b) Body mass data from all reproductively active males (open circles), redrawn onto a single 18-month period. Squares and lines show a simple model of annual mass change calculated assuming entry into hibernation on February 12 and arousal on July 2, with a mass loss during hibernation (grey bar) of 3.5 g·d^{-1}. A mass loss of 14 g·d^{-1} is assumed from arousal until the end of mating activity (shaded bar).

average dates of entry and arousal from hibernation and the mass losses given above. We have only limited data for females for the period between arousal from hibernation and entry into the nursery burrow. One female gained 328 g over 21 d, but others lost mass, possibly due to continued harassment by males, limiting feeding opportunities. For the model we have assumed no net change during this time. We have also assumed that females gain mass at a constant rate after emerging from the nursery burrow, but the graph shows many females continue to lose mass even after emergence. Our model assumes males lose mass from the period of arousal until the end of the mating season. Overall, this simple model provides a reasonable fit to the empirical data and shows the greatest mass losses are associated with reproduction and not hibernation.

GROWTH RATES AND LACTATION

Growth rates are of considerable interest because the hatchling is so small, and because of the echidna's low metabolic rate, which might limit maximum growth rates. Two hatchling echidnas from New South Wales weighed 0.38 g (Griffiths, McIntosh & Coles, 1969; Griffiths, 1978), while the mean mass of 11 newly hatched Kangaroo Island echidnas was 0.30 ± 0.03 g (Rismiller & McKelvey, 2003). After hatching, the growth of the young echidna can be divided into two phases. In the first phase the young is incubated in the pouch, and is able to suckle continuously. This phase ends when the young is evicted from the pouch, and from this point the young is left in a nursery burrow by the mother while she is feeding, and remains there until weaning.

The first measurements of echidna growth rates were made on a single young whose mother was held in captivity (Griffiths, 1978). In a study on free-ranging echidnas, Rismiller and McKelvey (2003) recorded the body masses of 25 pouch young between the ages of 5 and 60 d, and found similar growth rates to those observed by Griffiths (1978). From 5 to 55 d growth of young followed a typical mammalian power curve (Eisenberg, 1981) and could be described by the equation: body mass (g) = $0.27\text{age}^{1.607}$ (Rismiller & McKelvey, 2003). There are fewer data for the later stages of lactation and post-lactational growth. Figure 4 shows composite curves based on data from Rismiller and McKelvey (2003) combined with our own observations on 2 growing young and 8 y of observations on an adult. The growth curve follows a sawtooth pattern, with mass falling after weaning. Mass continues to fall through the first hibernation and does not increase until late in the following spring. As noted above, this annual fluctuation in mass continues through life, which makes it difficult to estimate when echidnas reach their adult size. Rismiller and McKelvey (2003) claim that Kangaroo Island echidnas do not begin reproductive behaviour until they are 5–12 y old, and the young Tasmanian male shown in Figure 4 (solid squares) was found with a female during his 6th year.

On Kangaroo Island the young are weaned when they are 204–210 d old (Rismiller & McKelvey, 2003). For 5 individuals followed from burrow life to post-weaning, body mass at weaning was 1.44 ± 0.48 kg (range 0.7–2.1 kg) and correlated with maternal mass (mass of young at weaning = maternal mass × 0.73 − 1.12; Rismiller & McKelvey, 2003). Abensperg-Traun (1989) monitored a young of the Western Australian subspecies (*T. a. acanthion*) and found weaning to occur at 195–200 d. At this point the young weighed 1.68 kg and the mother 3.8 kg. We have only been able to follow 2 burrow young through to weaning, and for 1 of these we have growth details (Figure 4, solid circles). This young was weaned at 153 d old, at which time it weighed 1.74 kg. The second was weaned at 146 d, with a mass of 1.55 kg. Maternal masses when the young were weaned were 4.16 kg and 3.68 kg, respectively, reasonably close to the relationship found by Rismiller and McKelvey (2003). The ratio of the mass of the young at weaning to average adult mass is about 0.4, a little higher than the average value for mammals (Charnov, 2002). However, time to weaning (150 d) is much shorter in Tasmania than that found for Kangaroo Island and Western Australian echidnas,
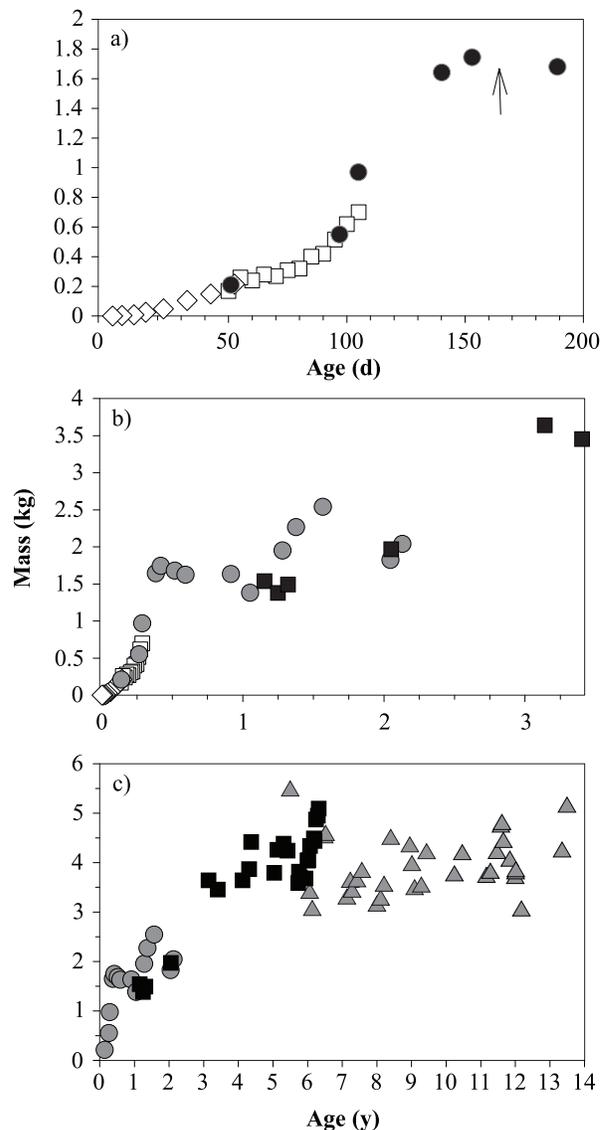

FIGURE 4. Composite growth curves for echidnas. Open symbols are data from Rismiller and McKelvey (2003) for 5 to 60 d (25 individuals, open diamonds) and 50 to 110 d (1 individual, open squares). Solid symbols are from our own observations on 2 growing young (solid circles and squares) and 8 y of observations on an adult (5D5E, solid triangles). The 3 panels emphasize the period of exponential growth up until weaning (arrow, panel a), the sawtooth growth of the juvenile (panel b), and the large annual variation in mass after adult mass is reached at about 4–5 y of age (panel c).

implying a significantly higher growth rate. This is necessary because in Tasmania the majority of matings occur in late July, and a 200-d lactation period would mean the young would not be weaned before mid-March, when the majority of animals have entered hibernation.

In an extensive analysis of 829 species from the 3 mammalian orders, Hayssen (1993) found the primary influence on lactation length to be female mass, with important constraints being imposed by phylogeny. The long lactation period of the echidna cannot be explained simply by the altricial nature of the young: marsupials, bats, and primates also have long lactation periods, but neither bats nor primates have particularly small offspring relative to maternal

mass, while dasyurid marsupials have shorter lactation periods than macropod marsupials, although dasyurid young are more altricial (Hayssen, 1993). As shown in Table II, the lactation period of echidnas is about 5 times longer than that of marmots, and echidnas are proportionately heavier at weaning. As Hayssen (1993) has pointed out, lactation in monotremes and marsupials, but not eutherians, encompasses the exponential period of offspring growth. In the echidna the highest absolute ($g \cdot d^{-1}$) growth rates occur just before weaning. The highest rate we have observed was an increase from 550 to 970 g in 8 d, an average of 41 $g \cdot d^{-1}$. By comparison, the highest growth rates observed in individual juvenile marmots (30 $g \cdot d^{-1}$) were post-weaning (Andersen, Armitage & Hoffman, 1976). In the period just before weaning, the lactating female echidna is supplying energy to her young at a similar rate to a female marmot with a litter of 4 with an average growth rate of 10 $g \cdot d^{-1}$.

The only measurements of field metabolic rates of lactating echidnas are from females with young aged 46–55 d, growing at about 5 $g \cdot d^{-1}$ (Schmid *et al.,* 2003). A mass increase of 5 $g \cdot d^{-1}$ would require the transfer of about 190 $kJ \cdot d^{-1}$ of milk energy (Green, Griffiths & Newgrain, 1992), amounting to about 25% of the field metabolic rate of a non-lactating echidna (Schmid *et al.,* 2003). Despite this, there was no significant difference in field metabolic rate between lactating (257 ± 30 $kJ \cdot kg^{-1} \cdot d^{-1}$, $n = 3$) and non-lactating females (227 ± 14 $kJ \cdot kg^{-1} \cdot d^{-1}$, $n = 4$), implying that there is a compensatory reduction in energy expenditure in other areas, such as gross activity or thermoregulation. At the end of lactation, however, the high growth rates of the young would be expected to approximately treble FMR, which is consistent with the observation that late lactation is the most energetically demanding time for a female mammal (Millar, 1977; Kenagy *et al.,* 1990; Speakman & McQueenie, 1996). What makes this period of the echidna life cycle particularly worthy of further study is the fact that despite this huge increase in metabolic demand, females increase in mass during late lactation (Schmid *et al.,* 2003).

The very low mass of the young at hatching, and the low initial growth rates (Figure 4) mean that the majority of maternal investment in the young is deferred until late lactation. The loss of an egg, or the loss of a young in the first few months of lactation, thus does not represent a large amount of lost energy investment in itself, and the female will have incurred a larger energy penalty by losing feeding time while she was in the burrow.

The majority of studies suggest weaning in echidnas is an abrupt event, with the mother opening the entrance to the nursery burrow, which is usually closed during her absence (Abensperg-Traun, 1991; Rismiller & McKelvey, 2003), and having no further contact with the young. This picture of a naïve young echidna having to learn how to forage for food by itself, and with no transition period while it still has access to milk, is supported by the loss of mass before the first hibernation (Figure 4). However, Abensperg-Traun (1989) reports a young excavating a shelter with its mother 67 d after weaning and then attempting to suckle. On 2 occasions in February we have found young echidnas (1.6 and 1.9 kg) in close proximity to an adult female we have assumed to be the mother. It is possible that these were chance encounters between a mother moving around her home range and a young that had not yet dispersed, but the behaviour around the weaning period is worth further study.

LIFE SPAN AND MORTALITY

An echidna (of unknown age when obtained) is recorded as having lived for 50 y in the Philadelphia Zoo (Crandall, 1964). In a compilation of longevity of captive mammals (Eisenberg, 1981) this was exceeded only by 57 y for an Asian elephant. Rismiller (1999) records an anecdotal report of an individual echidna living for up to 45 y in the wild, and while records for single individuals, particularly those in zoos, may be unrepresentative of average maximum longevity (Speakman *et al.,* 2002), it is clear that echidnas are very long lived mammals. As is typical of biological time periods the life span of mammals scales roughly as body mass$^{0.25}$ (McNab, 2002), and an allometric curve fitted to data from 47 mammalian species predicts the life span for a 4 kg mammal to be 17 y (95% confidence limits 12–26 y; Hofman, 1993). What accounts for the much longer than predicted life span of the echidna? As noted above, echidnas have a very low metabolic rate, and low T_b and low metabolic rates have been correlated with longevity in mammals (Austad & Fischer, 1991; White & Seymour, 2004; but also see Speakman *et al.,* 2002). Echidnas also use hibernation and torpor to further reduce energy expenditure, and Tasmanian echidnas spend 25–50% of any year at a T_b of less than 20 °C (Nicol & Andersen, in press). There appears to be a consensus that ageing is associated with the production of free radicals, and free radical production is proportional to metabolic rate (Lane, 2002). Although metabolic rate during hibernation is very low, in all hibernators the hibernation period is marked by periodic arousals to euthermic temperatures, which in echidnas occur on average at 11-d intervals (Nicol & Andersen, 2002). During these rewarmings metabolic rates reach at least 9 times basal (Nicol & Andersen, in press) and would be expected to result in significant free-radical production. Indeed, it has been demonstrated that there are significant periods of oxidative stress in the torpor–arousal cycle of hibernators (Carey, Andrews & Martin, 2003), and elevated levels of plasma ascorbate provide antioxidant protection during rewarming (Tøien *et al.*, 2001). While the idea that hibernation and torpor extend life span by slowing metabolism and free-radical production is probably too simplistic, the activation of stress resistance associated with torpor cycles may be associated with longevity (Stuart & Brown, 2006).

Echidnas also have a large brain with a large and extensively folded cerebral cortex, and on a graph of brain mass against body mass, the echidna lies significantly above the line describing therians (Hassiotis, Paxinos & Ashwell, 2003). Longevity has been shown to correlate with encephalization (Hofman, 1993), and the echidna encephalization index (0.066 ± 0.014) is similar to that of Carnivora (Hassiotis, Paxinos & Ashwell, 2003). Indeed, Hofman (1993) demonstrates that when the effects of body size, metabolic rate, and temperature are controlled for, brain mass is significantly associated with maximum life span in mammals, and suggests that selection for increased brain size results in a cascade of evolutionary effects, including single births, prolonged postnatal development and learning, a pro-

portional delay in maturation and reproductive rate, and thus an increase in generation time. An alternative explanation comes from the observation that endotherms with low exposure to environmental hazards and predation, and thus a low mortality, generally have long life spans (McNab, 2002).

For the majority of their evolutionary history, the principal potential predators of echidnas would have been large carnivorous marsupials and large reptiles. The thylacine and the Tasmanian devil were both widespread across Australia before the arrival of dingoes about 3000 y ago and quoll species occurred across much of Australia until relatively recently (Strahan, 1983). Varanid lizards (goannas) are still found across most of mainland Australia (Wilson & Knowles, 1992). By extrapolation from data on Kangaroo Island, where the principal predators are feral cats, pigs, and goannas (Rismiller & McKelvey, 2000), burrow young and sub-adults are the most susceptible to predation. An adult echidna when disturbed will rapidly move to the nearest refuge in rocks or logs, but if unable to reach a safe refuge, will dig into the substrate, presenting only its spine-covered back to the predator. Although echidnas often hibernate in easily accessible refuges, such as piles of leaf litter or grass tussocks, we have seen no evidence of predation of hibernating animals (Nicol & Andersen, 2006). In contemporary Australia, the major causes of morbidity and mortality of echidnas are motor vehicles and introduced predators (McOrist & Smales, 1986; Rismiller & McKelvey, 2000), and it is claimed that the majority of captive animals die from old age (Jackson, 2003).

In a stable population, recruitment will balance mortality, and as adult echidnas have a low mortality and a long life span, it is interesting to consider the limits on population growth. Firstly, reproductively mature female echidnas may hibernate through the breeding season (Nicol & Andersen, 2002). An estimate of breeding frequency can be obtained from T_b data from implanted data loggers (Figure 1). For the total of 32 y of T_b data we have from 7 adult females, they were reproductively active in only 15 (Nicol & Andersen, in press). Three females had young in 2 successive years, and 1 produced 4 young in 6 y. We do not know how many of these young survived to weaning. Rismiller and McKelvey (2000) recorded a lower rate of production, with 22 young being produced by 17 females over a 7-y period and only 8 surviving until weaning. The period immediately following weaning appears to be critical for young echidnas, which in Tasmania enter hibernation about 2 months after weaning. It also seems likely that there is significant mortality during dispersal.

Over a 7-y study on their *ca* 1000-ha Kangaroo Island study area (Rismiller & McKelvey, 2000) found 87 individuals, 17 of which (20%) were juveniles believed to have been recruited into the population from outside areas. Over 10 y on our similarly sized southern Tasmanian midlands study area we found a total of 168 individuals, 34 of which (20%) were juveniles. During the first 3 y we found 102 echidnas, and in following years new echidnas were found at a relatively constant rate of $9.7 \cdot y^{-1}$, with juveniles comprising 24% of these. Thus, it appears we have a resident population of about 100 echidnas with an annual turnover of about 10% and a recruitment of young echidnas of about 2.5% of the population.

Conclusion

Despite their near-ubiquitous Australian distribution, the echidna's relatively small size, cryptic habit, and long life have made it difficult to make estimates of life history parameters such as average life span and reproductive effort. It is also clear that there are significant differences between geographic populations or subspecies in such things as the length of lactation and the use of hibernation. There is however an accumulating body of information on the details of life history, allowing better insights into the relationship of these most successful of the egg-laying mammals with their environment. While it is reasonable to characterize echidnas as being at the extreme slow end of the fast–slow continuum, this should not obscure the fact that the mother can support remarkably high growth rates of young echidnas in late weaning while increasing her own mass.

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