PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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Phil. Trans. R. Soc. Lond. B 1998 **353**, 1081-1091
doi: 10.1098/rstb.1998.0267

The Royal Society

Field biology of the platypus (*Ornithorhynchus anatinus*): historical and current perspectives

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The field biology of the platypus, *Ornithorhynchus anatinus*, was first studied by a number of expatriate biologists who visited the Australian colonies to collect specimens in the 1800s. Their work was followed in the early to mid-1900s by a group of resident natural historians and later by an increasing number of academic biologists. All of these workers contributed significantly to the current understanding of the field biology of this unique Australian species. The platypus occupies much the same general distribution as it did prior to European occupation of Australia, except for its loss from the state of South Australia. However, local changes and fragmentation of distribution due to human modification of its habitat are documented. The species currently inhabits eastern Australia from around Cooktown in the north to Tasmania in the south. Although not found in the west-flowing rivers of northern Queensland, it inhabits the upper reaches of rivers flowing to the west and north of the dividing ranges in the south of the state and in New South Wales and Victoria. Its current and historical abundance, however, is less well known and it has probably declined in numbers, although still being considered as common over most of its current range. The species was extensively hunted for its fur until around this turn of this century. The platypus is mostly nocturnal in its foraging activities, being predominantly an opportunistic carnivore of benthic invertebrates. The species is homeothermic, maintaining its low body temperature (32 °C), even while foraging for hours in water below 5 °C. Its major habitat requirements include both riverine and riparian features which maintain a supply of benthic prey species and consolidated banks into which resting and nesting burrows can be excavated. The species exhibits a single breeding season, with mating occurring in late winter or spring and young first emerging into the water after 3–4 months of nurture by the lactating females in the nesting burrows. Natural history observations, mark and recapture studies and preliminary investigations of population genetics indicate the possibility of resident and transient members of populations and suggest a polygynous mating system. Recent field studies have largely confirmed and extended the work of the early biologists and natural historians.

Keywords: platypus; ecology; temperature regulation; habitat requirements; foraging; social organization

1. INTRODUCTION

Arrival of the first platypus specimens in Britain and Europe at the turn of the 19th century sparked two immediate controversies. The first, which concerned the authenticity of these skin preparations, was resolved quickly by their careful examination (Shaw (1799), cited in Harrison (1922)), and the subsequent arrival of whole spirit-preserved specimens (Home (1802), cited in Harrison (1922)). The second controversy concerned the mode of reproduction of this mammal-like species. The debate over the nature of reproduction in the monotremes centred around viviparity and the presence of functioning mammary glands and was encouraged by the opposing views of the eminent English anatomist Sir Richard Owen and the French biologist M. Etienne Geoffroy (Caldwell 1887; Harrison 1922). Although the presence of mammary glands was established by Meckel (Meckelio 1826), the debate over parturition was not finally settled until the work of a young Scotsman, William Caldwell, who visited the 'colonies' and conducted extensive field work on the platypus (Caldwell 1887). His efforts culminated in the famous telegram to the Montreal Meeting of the British Association in September 1884 confirming oviparity in monotremes (Caldwell 1884). The field observations of Caldwell and other expatriate naturalists became the first published information on the natural history of the platypus and represented the only written accounts of platypus field biology until a second wave of dedicated natural historians in the early to mid-1900s—in particular Harry Burrell (1927), Robert Eadie (Barrett 1944) and David Fleay (1944, 1980)—provided a new understanding of the biology of the species. Following this resurgence of interest, platypus field biology was largely neglected until the work of a few postgraduate students, including the authors (Temple-Smith 1973; Grant & Dawson 1978*a*,*b*), showed that modern field studies of this shy, semi-aquatic, mainly nocturnal, diving and fossorial species were possible. Since then, with an increase in the number of researchers engaged in field studies of the platypus and the use of new field techniques, such as radio-tracking and radio-telemetry, a new synthesis of the field biology of the platypus has emerged. Important advances have been achieved in the fields of population biology, distribution, thermoregulation, feeding ecology, social organization and habitat requirements. This review discusses the findings of recent studies in these and other areas against the background of the observations and data collected by the early European expatriate naturalists and the natural historians of the early 20th century.

2. DISTRIBUTION

Establishing the limits of its distribution is important to the understanding of the ecology of the platypus, especially its habitat preferences. Recorded changes in distribution with time often represent shifts in the conservation status of species due to the influence of natural or human-induced changes upon them. The changes wrought by slightly over 200 years of European occupation of the Australian continent have been profound and the distributions of many species of native animals have changed dramatically (Kennedy 1990).

Platypuses are found in rivers and streams flowing to the east and south coasts of eastern Australia, from around Cooktown in the north of Queensland to Tasmania (figure 1). In northern Queensland they are now only found east of the Great Dividing Range, although the species had been previously recorded in the Norman (Waite 1896), Leichhardt, and possibly the Gilbert (Armit 1878; Burrell 1927) rivers, which flow west into the Gulf of Carpentaria. As these records have not since been authenticated and the rivers concerned do not now appear to provide, and may never have provided, suitable platypus habitat, it has been suggested that these observations may have been of another species (Griffiths 1978), possibly the water rat, *Hydromys chrysogaster*. An expedition in 1976 failed to find any platypus in the east-flowing Rocky, Massey and Claudie Rivers and Peach and Cockatoo Creeks on the Cape York Peninsula. Interviews with local people also indicated that the species does not occur in the north of Cape York (T. R. Grant, F. N. Carrick and M. Griffiths, unpublished observations, cited in Griffiths (1978)). Water temperatures above the normal body temperature of the platypus (32 °C), extreme flooding during the summer 'wet' season and the presence of saltwater crocodiles, *Crocodylus porosus*, are all possible reasons for the absence of the species from potentially suitable rivers on Cape York, although these suggestions need further investigation (Griffiths 1978; Grant 1992*a*, 1995).

Platypuses do occur in the upper reaches of the west-flowing rivers in southern Queensland and New South Wales and in those flowing north from the dividing ranges in the state of Victoria. They are also found in the upper and middle sections of both the Murray and Murrumbidgee river systems and may have been more common in their middle reaches prior to the escalation and subsequent decline of commercial fishing operations, using small mesh nets, from around 1880 to the 1950s (Grant 1993). Illegal fishing continues to drown small numbers of platypuses in many streams throughout their distribution. The absence of the species from most rivers flowing through the western plains of eastern Australia has been attributed to the intermittent flow of these rivers during drought (Grant 1992*a*). The construction of storage reservoirs for irrigation purposes has resulted in many of these rivers now being supplied with more constant flows than occurred previously. However, platypuses have still not occupied the lower reaches of these regulated streams, suggesting that other habitat variables are involved. Complete inundation of the low-lying areas of the western plains during periodic flooding, the unsuitability of the river banks and their soils for construction of burrows and high summer water temperatures, especially during drought conditions, have also been suggested to explain why the distribution of platypuses is often restricted to the upper reaches of these rivers (Temple-Smith 1973; Grant 1995).

The species is common throughout Tasmania. It also occurs naturally on King Island in Bass Strait, north of Tasmania, and has been introduced to Kangaroo Island, off the coast of South Australia (Fleay 1980; Grant 1992*a*). The platypus was found in streams of the Mount Lofty Ranges, near Adelaide, and the Fleurieu Peninsula in South Australia until the mid- to late 1800s. It was probably never common in these areas, and the lack of specimens or confirmed sightings this century suggests that it has become extinct (Grant 1992*a*). Predation of platypuses by foxes and dogs is known to occur during the passage of animals through shallow or dry riffles of rivers and streams (Grant & Denny 1991; Serena 1994). It is possible that these introduced species may have caused or contributed to the decline of the platypus in this area of South Australia, where most rivers are reduced to series of isolated pools each year during late summer and autumn (Grant & Denny 1991). This possibility requires further investigation with regard to the effectiveness of proposed reintroductions of the platypus to that state. There is no evidence that the species has ever been an inhabitant of Western Australia.

Over its distribution (figure 1) the species occupies a wide range of climatic conditions, from tropical to cool temperate and including mountain and tableland areas that have cold winter temperatures. The early naturalists observed or captured platypus in all of the states in which they now occur (Grant & Denny 1991; Grant 1992*a*) and the range described by Burrell (1927) is almost identical to that of the present distribution. Whereas the platypus appears to still occur over most of the area in which it was found before European occupation of Australia, nothing is known of the numbers that may have been present. Certainly large numbers of individuals were taken for their furs by commercial hunters before their protection in all states around the turn of the century (Grant & Denny 1991; Grant 1992*a*). Local reductions in distribution have been reported, especially around the metropolitan areas of Melbourne, Sydney and Brisbane (Grant & Denny 1991; Grant 1992*a*, 1998). Bennett (1860) obtained many of his specimens from streams flowing through what are now the far western settlements of the greater Sydney area, including the spot where Governor Hunter observed a party of Aboriginal people spearing a platypus in 1798 (Home 1802), and an area where the species is only occasionally seen today (Recher *et al*. 1993; Rosen 1995; Grant 1998). There is also now evidence of the fragmented distribution and local reductions in numbers of platypuses in areas where poor land management practices have resulted in marked changes

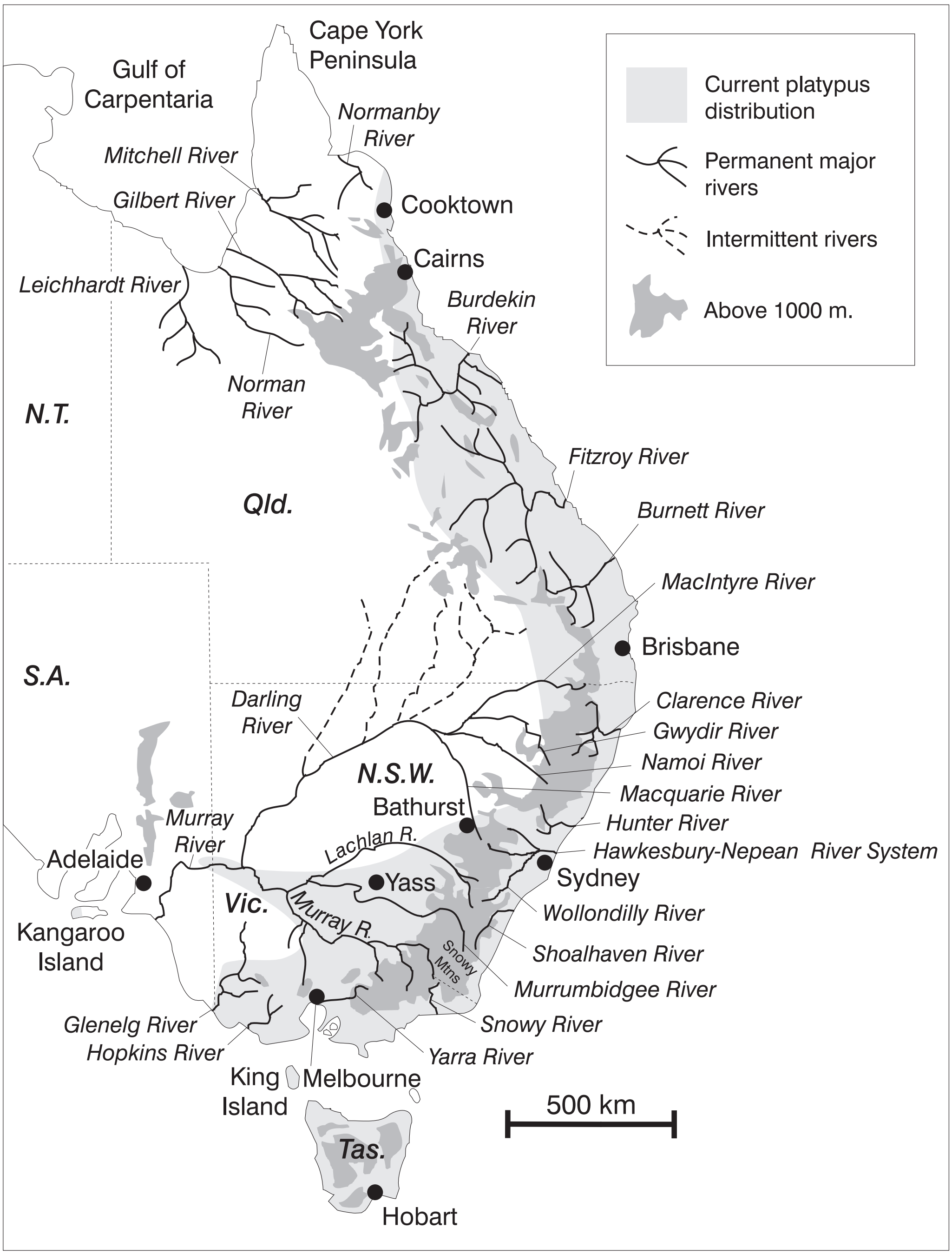

Figure 1. Distribution of the platypus. The overall distribution is shaded. Major features, including towns and rivers, referred to in the discussion are also shown. N.T., Northern Territory; Qld., Queensland; S.A., South Australia; N.S.W., New South Wales; Tas., Tasmania.

to platypus habitats (Rohweder 1992; Brooks & Brierly 1996; Lunney *et al.* 1998). On the other hand, recent diligent searching in some severely degraded streams around the Melbourne metropolitan area has located small populations of platypus (Serena 1996) and individuals have been captured in other highly degraded streams near human settlement (e.g. Grant & Denny 1987), indicating the resilience of the species.

3. ABUNDANCE

On a trip to the western settlement of Bathurst in 1815, Governor Macquarie reported 'great numbers of water moles in the Campbell-River at Mitchell Plains' and two were brought back to camp from the Fish River after an evening's fishing by Sir John Jamison (Macquarie 1956). Caldwell (1887) also indicated that they were 'very numerous' in 1884 in the Burnett district of Queensland, and Semon (1899) noted catching 'a considerable quantity' in the same area in winter, although he had less success during summer when he suggested they emerged when it was too dark for hunting. However, Bennett (1835) made no comment on the abundance of the species in the Goulburn, Yass and Tumut areas of New South Wales. Whatever their abundance before European occupation of Australia, platypuses are reputed to have declined in numbers during the days of trade in their furs, before their protection in all states by 1912 (Gould 1863; Wilson & Hill 1908; Burrell 1927; A. T. 1946; Grant & Denny 1991). Since then, populations are reported to have increased in number (Barrett 1944; A. T. 1946), but there is no objective evidence available to support this suggested increased abundance since that time. Because of the thickness of the skin and its resultant stiffness after tanning, skins were not in demand for clothing; most were used locally to make hats, slippers and rugs (Gould 1863; Burrell 1927; Grant & Denny 1991). However, as a single rug comprises between 40 and 60 pelts (Barrett 1944; Grant & Denny 1991), large numbers of platypuses must have been killed during the period in which the species was hunted. Ward (1966) notes that a local resident of a suburb of Melbourne around 1870, made 'a fairly good living' by selling platypus skins to local furriers. Burrell (1927) records that 'one of two brothers who were both great hunters of platypus, confesses to having been wicked enough to have shot many thousands during his thirty-two years of work'. Burrell (1927) also detailed a report of the apparent migration of 'at least' 100 platypuses along the Gwydir River after a flood in 1859, although no such phenomenon has been recorded since.

Only two scientific estimates of numbers have been published for platypus populations. Grant & Carrick (1978) used mark and recapture data to estimate a minimum population of 14–18 individuals occupying approximately 1.5 km of two large river pools connected by a long riffle sequence in the upper Shoalhaven River, a perennial coastal river in New South Wales. Animals were captured using unweighted fishing ('gill') nets that entangle animals and permit them to surface to breathe. This method is only suitable in stationary pools or slow-flowing water (Grant & Carrick 1974). A much larger number of animals were subsequently captured in this location, differential catchability of individuals and/or between sexes was apparent and some loss of bands also occurred during the study. Grant (1992*b*) discussed the difficulties of making accurate population estimates using mark and recapture information from netting operations for this species, which appears to exhibit considerable mobility and differential catchability. During a radio-telemetric study of body temperature of five platypuses during winter in the Thredbo River in the Snowy Mountains area of New South Wales, netting operations failed to capture some radio-tagged individuals in pools where they were known to have spent most of their time during the study period (Grant 1992*b*; Grigg *et al*. 1992). Netting of artificial ponds within the confines of Warrawong Sanctuary in South Australia also failed to capture individuals that were known to inhabit these ponds and to have contributed to the genetic complement of offspring born in the system (Gemmell *et al*. 1995).

Serena (1994) used a series of fyke nets to capture foraging platypuses during a radio-tracking study along a small stream at Healesville, near Melbourne, Victoria. These nets consist of a wind-sock-shaped bag with several constrictions (or 'valves') preventing the escape of platypuses that enter the nets. Mesh wings from each net are stretched across the small streams to direct foraging platypuses into the nets, which are set in pairs with one facing upstream and one downstream. This technique is most suitable for small streams (Serena 1996). Assuming that the method captured the entire population moving through or within the study area, Serena (1994) estimated a population of 1.3–2.1 adult individuals per kilometre of stream. Platypuses, however, are known to leave the water to move around obstructions (Burrell 1927; Grant & Denny 1991; D. Goldney, personal communication) and may bypass nets, so even this method may not yield accurate population estimates in all instances of its use.

A number of workers have used visual observations to assess presence or absence of the species in an area. The numbers of individuals observed at one time can be used as a measure of broad categories of abundance, such as 'rare', 'common' or 'abundant' (Grant 1992*b*; Rohweder 1992; Bryant 1993; Woon 1995). However, observations and netting together show that lack of observation may not necessarily indicate absence of the species from an area because platypuses have been captured at locations where local people have indicated that the species is absent (T. R. Grant, unpublished data).

Although data from netting, observations and community-based questionnaire surveys suggest a reduction in local distribution and numbers of platypuses due to human activities (Rohweder 1992; Grant 1998; Lunney *et al*. 1998), accurate quantitative data on population sizes are no more available now than they were in the times of the early naturalists. Taken together, however, the data suggest that the platypus was probably more abundant before European colonization and that commercial hunting for pelts, followed by the continuing and increasing disturbance of habitat caused by poor land management practices, such as farming and forestry, have resulted in population declines.

4. FOOD AND FORAGING ACTIVITIES

The stomach of a platypus is extremely small (Griffiths 1978), so that an early report by Jamison (1818) of 'small fish and fry' being found in the stomach is probably erroneous, and information regarding food consumed by the species has been from the investigation of the contents of cheek pouches, which lie beside the horny grinding pads that replace the teeth in newly emerged and adult animals. Food items are stored in these pouches during foraging but are then masticated and finely ground by the time they are ingested, so that the majority of material in the digestive system is not recognizable. The presence of benthic invertebrate species, especially insect larvae, in the cheek pouches have been noted by most investigators (Bennett 1835; Crowther 1879; Allport 1878; Semon 1899; Burrell 1927; Fleay 1944; Faragher *et al*. 1979; Grant 1982), although free-swimming species, such as shrimps (Crowther 1879; Fleay 1944; Faragher *et al*. 1979), crayfish (Burrell 1927; Fleay 1944, 1980), beetles (Crowther 1879), water bugs (Burrell 1927), and tadpoles (Fleay 1944), also appear to be included in the diet. After watching a platypus foraging in the gravel bottom of a stream in Tasmania during the spawning season of the grayling, Allport (1878) indicated that the species may take fish eggs and indicated that he could not 'conscientiously recommend the owners of trout streams to encourage the presence of *Ornithorhynchus anatinus*'. Trout streams are not 'owned' in Australia and fortunately this advice was not heeded. Recruitment from spawning in the wild and artificial stocking seem to have maintained trout populations in most suitable streams where their range has overlapped that of the platypus for over 100 years (Faragher 1986), even though platypuses have been shown to eat trout eggs in the wild (Anonymous 1945; Grant 1982). In the confinement of a tank environment, captive platypuses will catch and consume mosquito fish (*Gambusia affinis*) and small goldfish (*Cyprinus carpio*) (Grant *et al*. 1977; Carrick *et al*. 1982; Krueger *et al*. 1992). Anecdotal observations have been made of the platypus consuming trout fingerlings of up to 3 inches (*ca*. 7.6 cm) in length (Nicholls 1958), but this has not yet been confirmed by other field observations. The introduction of a variety of salmonid fish species (mainly *Salmo trutta* and *Onchorhynchus mykiss*) into the rivers and lakes of Australia has probably inadvertently benefited the platypus, in spite of some overlap in their diets (Faragher *et al*. 1979). Outlawing the netting of fish in rivers, by such legislation as the 1902 Fisheries Act in New South Wales, was aimed at the conservation of introduced salmonid species, but also must have reduced the incidence of the drowning of platypus (Faragher 1986; Grant 1993). There have been several suggestions that the species may eat vegetation (Bennett 1835, 1860; Burrell 1927), but these have not been substantiated. Historical observations and recent work are both in agreement with the general conclusion that the platypus is mainly an opportunistic consumer of benthic invertebrate species.

Platypuses dive repeatedly during foraging, spending short periods between dives on the surface while masticating food items. Observations of this behaviour were often made by the early naturalists in reference to the species being difficult to shoot, owing to the short period spent on the surface, and the animal's rapid diving in response to the slightest movement or noise on the bank (Bennett 1835, 1860; Semon 1899; Burrell 1927). Diving times have been reported by both early naturalists and recent field biologists at between 30 s and 3 min, with generally a shorter period spent on the surface between dives (Allport 1878; Burrell 1927; Kruuk 1993; McLeod 1993; Grant 1995). A laboratory study of diving physiology showed that the platypus relies on oxygen content of the air in its lungs during diving, rather than that stored in myoglobin, as occurs in other specialist diving mammals. The captive individuals in this study also showed marked diving bradycardia, an ability to inspire a large quantity of air prior to diving and the capacity for dives longer than those recorded in field observations (Evans *et al*. 1994). Kruuk (1993) used a ratio of time under water to time on the surface as a measure of foraging efficiency in the platypus, which normally needs to collect several small food items during each dive, rather than single large prey items (Faragher *et al*. 1979; Grant 1982). He indicated that foraging efficiency was increased in eutrophic waters, owing to a presumed high abundance of benthic invertebrates, but also found that the distances covered during foraging dives were greater in his eutrophic sites than in the more oligotrophic ones. Although often statistically significant, the actual differences in dive times were quite small. In addition, the abundance of benthic organisms was not measured during this work, but taken from a previous study, and no benthic invertebrate data were available for one of the sites considered. These are limitations of the study, which also failed to give adequate consideration to the effects on foraging behaviour of the normally mosaic nature of benthic invertebrate distribution (Hynes 1970; Elliott 1977). However, the study does give support to the notion that platypuses are indeed opportunistic in their foraging. This is also supported by observations of platypuses commonly occurring downstream of sewage effluent outfalls into some inland rivers, where tolerant species of benthic invertebrates are normally abundant but where there is reduced diversity of benthic organisms (Grant 1991).

Early observations indicated the apparently crepuscular nature of the foraging of platypuses in the wild (e.g. Bennett 1835, 1860; Semon 1899; Burrell 1927), while more recent studies (using modern radio-tracking technology) have shown continuous or intermittent activity throughout the night, with daytime activity in some individuals (Grant 1983*a*; Grigg *et al*. 1992; McLeod 1993; Serena 1994). However, closer inspection of the writings of the early biologists and naturalists shows that they tried and were unable to observe animals during the night, but suspected that they indeed were active in the water during the hours of darkness (Semon 1899; Burrell 1927). Platypuses are known to forage over distances of up to 4 km during a 24-h period (Grant 1983*b*; Grant *et al*. 1992; Serena 1994) in river systems. Recently, the foraging area of three radio-tracked platypuses in Lake Lea, an alpine lake in Tasmania, was found to be 14–30 ha ($1\,\text{ha} = 10^4\,\text{m}^2$), and some individuals in this population were diurnally active, whereas others were nocturnal (Otley *et al*. 1996). Differences in the foraging activities of individuals and between areas may be related to social organization in populations, or possibly to the activity and availability of benthic food organisms. The former suggestion is discussed later in this review but the latter has not yet been investigated.

5. TEMPERATURE REGULATION AND HIBERNATION

As indicated previously, part of the range of the platypus covers the tableland and even alpine regions of eastern Australia. Its dependence on benthic invertebrate species for its food means that in these areas individuals must enter water at temperatures that may be as low as 0 °C during winter (Grant 1983*b*). In 1897, Sutherland, using an average of three measurements made by Baron Maklouho-Maclay on one individual platypus (Grigg *et al*. 1992), stated that 'the platypus, therefore, at 24.8 °C is almost a cold blooded animal'. This gave support to the idea of phylogenetic primitiveness in the monotremes. Early in the 20th century, however, both naturalists (Burrell 1927) and biologists (Martin 1902) concluded that, although the platypus did have a low body temperature when compared with other mammals (32 °C), it was capable of maintaining this temperature over a range of air temperatures. However, the ability of the species to maintain homeothermy in water was doubted. No supporting evidence was given by Martin (1902), but he commented on the ability of the platypus to regulate its body temperature in water thus: '*Ornithorhynchus* is not an amphibious animal, and only goes into water for food or to amuse itself, and if kept too long in water its temperature falls and it dies'. Burrell (1927), who spent inordinate amounts of his time observing platypuses in the wild, agreed with this conclusion. Studies of captive platypuses (Grant & Dawson 1978*a*,*b*), and radio-telemetric work on free-ranging animals (Grant 1983*b*; Grigg *et al*. 1992), have shown the erroneous nature of these earlier conclusions, as platypuses were found to maintain homeothermy while foraging for hours in water below 5 °C. A constant body temperature is maintained in actively foraging animals by an increase in their metabolic activity, the excellent fur and tissue insulation and the possession of a vascular counter-current heat exchange system at the base of the hind legs and tail (Grant & Dawson 1978*b*).

Bennett (1835, 1860) indicated that platypuses could be seen in Australian rivers at all seasons of the year, but because of his observations that the species was more abundant in summer than in winter, he speculated on the possibility that individuals may 'not in some degree hybernate'. Burrell (1931) referred to periods of absence from the river, such as might occur during flood flows, as 'lethargy-at times confused with true hibernation'. Eadie (1935) and Fleay (1980) recorded animals in captivity remaining in their nesting quarters for periods of up to 6.5 days and inferred that they were hibernating or in a torpid state. A number of radio-telemetered individuals, monitored during winter in the Shoalhaven and Thredbo Rivers in New South Wales, showed no evidence of hibernation or torpor (Grant 1983*b*; Grigg *et al*. 1992), but similar observations to those of Fleay and Eadie were made by Serena (1994) during winter in radio-tracked wild animals. Unfortunately, the body temperatures of these latter animals were not measured and the possibility of torpor or hibernation during periods of inactivity recorded by Eadie, Fleay and Serena still needs to be resolved.

Platypuses have been known for some time to be intolerant of temperatures higher than 25 °C (Martin 1902; Robinson 1954), but individuals in the field normally avoid such temperatures, even in the tropical parts of their distribution, by occupying burrows where the insulation of the soil buffers the changes in ambient temperature inside the burrow. Grant & Dawson (1978*b*) found that the temperature inside an artificially constructed platypus burrow remained between 14 and 18 °C while the outside air temperature in their study area went from −5.5 to 33.5 °C during the same period. Although the cooling capacity of water means that high thermal stress does not generally occur while individuals are foraging in water, the loss of metabolic heat produced during exercise in water at temperatures higher than the normal body temperature of the species means that animals cannot tolerate such water temperatures (Grant & Dawson 1978*a*,*b*). Thermal stress during foraging in water may be a factor involved in the limited distribution of the platypus in the tropical north of Australia, especially on the Cape York Peninsula, where suitable habitat seems to be available (T. R. Grant, F. N. Carrick and M. Griffiths, unpublished observations, cited in Griffiths (1978)), and in the rivers of the western plains areas of eastern Australia.

6. HABITAT REQUIREMENTS

'Soon the river was before me, the banks of which were adorned by pendulous Acacias, which at this season of the year [September] were profusely covered with their rich golden and fragrant blossoms, while the lofty majestic *Eucalypti* or Gum-trees, many of which were young and gracefully pendent, together with the Swamp Oaks or *Casuarinaea*, resembling firs at a distance, added to the variety and natural beauty of the landscape'. So George Bennett (1860) described the Yass River in New South Wales, where he shot platypuses in his quest to determine their mode of parturition. Today the banks of the Yass River in the same area have been severely damaged by the hooves of cattle and are vegetated mainly by introduced willows (*Salix* sp.), whose roots have resulted in narrowing of the river channel. A few of the *Eucalypti* (*Eucalyptus camaldulensis* or river red gum) and swamp oaks (*Casuarina cunninghamiana*) are still present, and ribbonweed (*Vallisneria gigantea*), also noted by Bennett still occurs, as does the 'shy *Ornithorhynchus paradoxus* [*anatinus*]'.

In his verbal sketch of the banks of the Yass River, Bennett was describing one of the key habitat requirements of the platypus. It is in earth banks consolidated by roots of the associated vegetation that the species can dig both the short resting burrows (Burrell 1927; Grant 1983*b*, 1995; Serena 1994) and the longer and more complex, breeding burrows, where the suckling young remain for three to four months after hatching from the egg (Burrell 1927; Temple-Smith 1973; Grant & Griffiths 1992; Grant 1995). While Bennett (1835, 1860) gave illustrations of excavated burrows, an excellent description of platypus habitat was given by Lieutenant the Hon. Lauderdale Maule of the 39th Regiment, stationed on the Fish River, near Bathurst in New South Wales, in the spring of 1831, in his letter to the Committee of the Zoological Society of London (Maule 1832). It read: 'The *Platypus* burrows in the banks of rivers, choosing generally a spot where the water is deep and sluggish, and the bank precipitous and covered with reeds or overhung by trees'. Similar descriptions of typical platypus habitat have been commonly associated with the occurrence of platypus (e.g. Semon 1899; Kershaw 1912; Burrell 1927; Fleay 1944). Such descriptions also include many of the characteristics distinguished by a number of recent field investigations aimed at elucidating the fine detail of the biophysical parameters which constitute suitable habitat requirements of the species (Rohweder 1992; Bryant 1993; Woon 1995; Ellem *et al*. 1998). These studies have used a number of statistical analyses to match a wide range of physical features and water quality parameters to the observed presence or absence of platypuses in a number of streams in New South Wales. Although the lack of observation of platypuses in an area does not necessarily mean that they are definitely not present (T. R. Grant, unpublished data), the use of presence or absence data in these studies has highlighted the habitat features that are most often associated with the presence of platypuses, and therefore those that are important to the species. The 'ideal' platypus habitat identified by these studies is a river or stream with relatively steep earth banks consolidated by the roots of native plant species whose foliage overhangs the banks. The river or stream itself has a diversity of habitats, including aquatic vegetation and logs, and consists of a series of distinct pools of less than 5 m in depth, with little sand accumulation, and separated by cobbled riffle areas—very similar to the habitat description given by Maule (1832), nearly 170 years previously.

These features can now be identified as being important in supplying the resource needs of the platypus, which mainly occupies burrows in earth banks when it is not foraging in the water (Burrell 1927; Grant 1983*b*; Serena 1994). These are normally dug into earth which is consolidated by the roots of riparian vegetation. The presence of riparian vegetation overhanging river banks has been identified in all three studies as an important habitat requirement of the platypus (Rohweder 1992; Bryant 1993; Woon 1995; Ellem *et al*. 1998). This is probably due to the shelter provided for individuals foraging in the stream near the bank and permitting safe access to burrow entrances. Overhanging vegetation also has an important influence on water temperature and photosynthetic productivity, provides organic material for benthic shredder organisms and creates habitat diversity for benthic invertebrate species in the stream (Cummins 1993; Riding & Carter 1992). Some platypuses will move to the water from burrow entrances a metre or so from the water level, although such burrow entrances have usually been reported or found among sheltering vegetation (T. R. Grant, unpublished data). Normally the entrances of platypuses' burrows are close to (Burrell 1927; Fleay 1980; Grant 1983*b*, 1995), or below, the water level (Serena 1994). As platypuses move relatively slowly on land they are susceptible to predation, especially by introduced foxes, when not in the water (Grant & Denny 1993; Serena 1994). As a consequence, the presence of a consolidated earth bank immediately adjacent to the water is an important habitat variable.

There are a large number of habitat variables that influence the production of benthic invertebrate species, which are the major food resource of the platypus (Faragher *et al*. 1979; Grant 1982). These include biotic variables, such as logs, twigs, roots, and in-stream vegetation, as well as abiotic ones, including substrate types. Higher invertebrate productivity is usually associated with areas where logs, roots and vegetation provide a range of habitats for different invertebrates and where a cobbled or gravel substrate provides fixed habitat, rather than shifting substrates, such as sand (Hynes 1970; Marchant *et al*. 1984). The complexity of benthic habitats (Rohweder 1992), and the presence of aquatic vegetation (Bryant 1993; Woon 1995), have both been shown to be indicators of the occurrence of platypuses. Platypuses feed both in pools and riffles and the identification of sequences of these being associated with the presence of the species is related to their higher productivity, with riffles normally being more productive than pools (Hynes 1970). Grant & Bishop (1998) have discussed the importance of the measurement of these habitat variables in relation to the assessment of the instream flow requirements of stream biota, including the platypus, during the environmental impact assessment of proposed riverine and riparian developments.

Although the important stream and riparian zone characteristics identified by the studies of Rohweder (1992), Bryant (1993), and Woon (1995), occur most often in areas with the least human disturbance, platypuses can be found in a wide range of habitats, both pristine and degraded, showing the remarkable adaptiveness of the species. As discussed earlier in this review, small populations have been identified in severely disturbed streams around Melbourne (Serena 1994) and the species is still occasionally reported close to the Sydney metropolitan area (Grant 1998). However, the long-term effects of such degradation on the local distribution and abundance of the species are as yet not fully known.

7. SOCIAL ORGANIZATION AND MATING SYSTEM

Platypuses are seasonal in their breeding activities. Throughout their range, breeding times are spread within populations and appear to be earlier in the northern parts of the distribution and later in the south (Griffiths 1978; Grant 1989). In New South Wales, platypuses mate in late winter or autumn and young first appear in streams in January or February, after gestation and incubation periods of unknown length (but probably around 27 and 10 days, respectively), and a lactation period of between 3 and 4 months (Temple-Smith 1973; Griffiths 1978; Grant *et al*. 1983; Grant & Griffiths 1992; Grant 1995). The minimum recorded age at first breeding in a female platypus is in the second breeding season, but some juvenile females do not breed until at least their fourth year of life, and some individuals do not breed in each consecutive year after they have first bred (Grant & Griffiths 1992). Nothing is known of any social organization that may govern the reproductive activities of females within platypus populations.

Presumably because they were mainly interested in obtaining animals in the quest to determine the nature of their parturition or in the study of their anatomy, the early expatriate biologists and natural historians recorded few observations of platypus behaviour in the field. Burrell (1927) indicated that 'except during the breeding season, platypus may be considered solitary animals', although he did record burrow sharing between males. Burrow sharing has also been recorded in radio-telemetry (Grant *et al*. 1992) and radio-tracking studies (Serena 1994). Male platypuses do not produce functional spermatozoa until their second year and presumably begin to breed at that time (Temple-Smith 1973). The adult male crural system, consisting of a pair of venom glands attached by ducts to hollow spurs on each rear ankle (figure 2), is used to inflict painful injuries on other platypuses, humans and potential predators. Although the presence of the spurs and secretions of the crural gland in males has been variously attributed to climbing of river banks (Axford 1829), collection of nesting material (Burrell 1927), waterproofing the fur (Spicer 1876), holding the female during copulation (Home 1802; Burrell 1927), or as a weapon of defence (Burrell 1927), most evidence supports the idea first proposed by Martin & Tidswell (1894) that 'the idea naturally occurs to one that this apparatus, which is confined to the male sex, owes its peculiar development to the operation of sexual selection. That it is a weapon used by males on one another when conflicting for possession of the females, is an idea which would become extremely probable if it could be established that the gland is specially developed at or about the pairing season'.

Temple-Smith (1973) found that the crural gland and testes increased and decreased in size before and after the mating season (figure 2). Males become more aggressive when handled and individual males are often found in

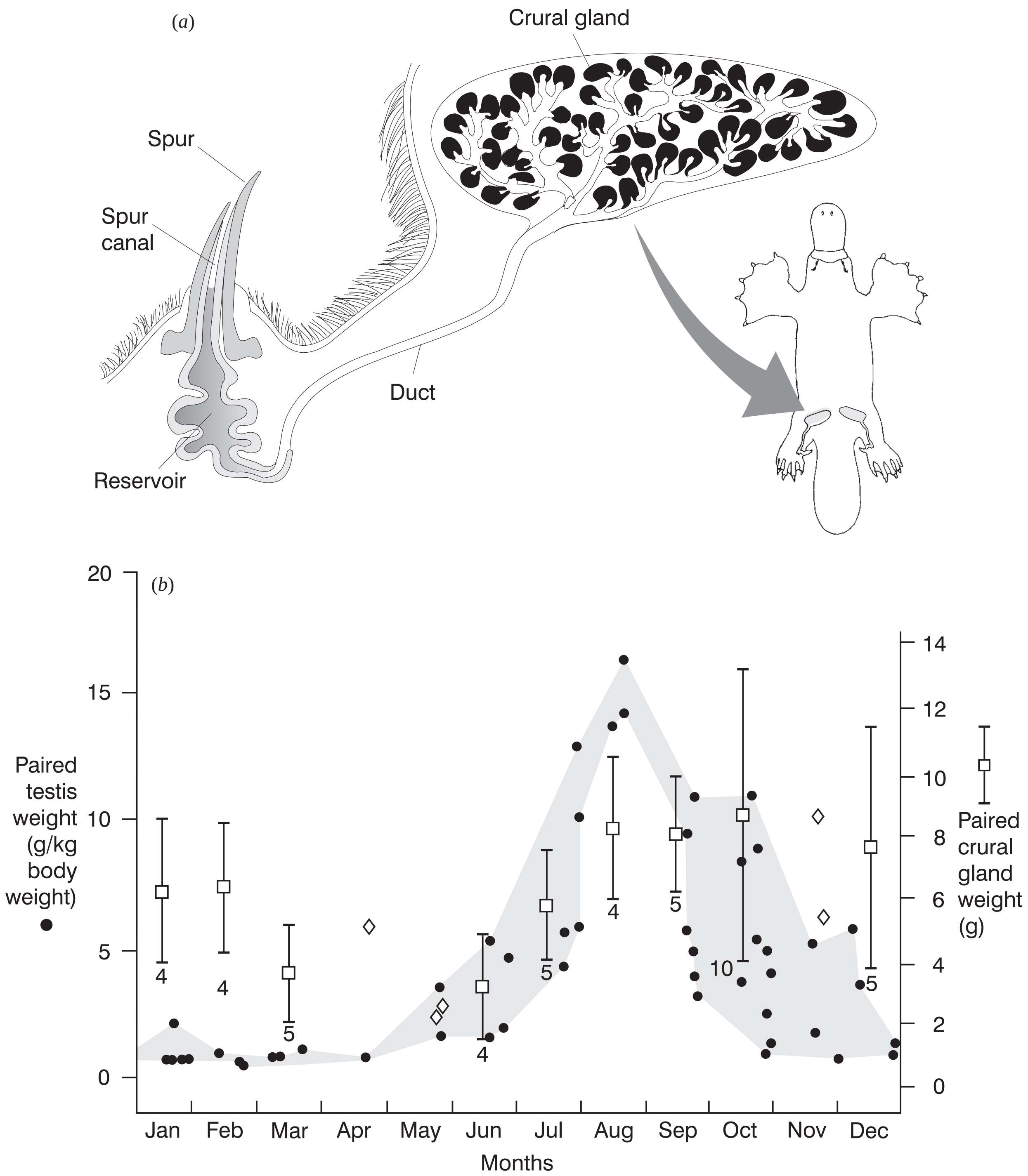

Figure 2. The crural system. (*a*) The structure and position of the components of the crural system. (*b*) Seasonal changes in the weights of the paired crural glands (means, standard deviation and numbers of animals in sample are shown; diamonds represent individual animals) and testes (individual values shown; shading covers the range of values).

the wild with punctures in their bodies (especially in the tail region) during this period (Temple-Smith 1973; Grant 1995, unpublished data). Radio-tracking in two locations in the Yarra River catchment near Melbourne showed overlap of the home ranges of adult females, subadult and adult males and juveniles. The home ranges of some adult males were, however, either mutually exclusive from other adult individuals or when overlap occurred, adult males largely avoided each other (Serena 1994; Gardner & Serena 1995). Whereas overlapping home ranges of adult male platypuses in the Goulburn River, Victoria occurred during the non-breeding season, there was evidence of temporal separation of these individuals in the breeding season (Gust & Handasyde 1995). These observations suggest support for the notion that development or retention of the crural gland and spur in the male platypus is related to sexual selection (Martin & Tidswell 1894; Temple-Smith 1973), possibly involving a polygynous mating system with access to females being maintained by the results of male–male interactions. Sexual dimorphism, where male platypuses are normally 40% heavier and 10% longer than females, also suggests polygyny. Preliminary results from genetic studies of the Shoalhaven River population (Akiyama *et al*. 1996) do in fact indicate polygyny, but with sneaking by males not regularly captured in the area.

Using the results of mark and recapture studies of platypuses in the upper Shoalhaven River in New South Wales, Grant (1992*b*, 1995) suggested the occurrence of a resident group, which was regularly recaptured, along with a more transient group consisting of animals captured only once and ones caught a number of times, but often with intervals of several years between captures (T. R. Grant, unpublished data). In studies on the upper Shoalhaven River, New South Wales (Grant 1992*b*), and Badger Creek, Victoria (Serena 1994), lower recapture rates of juvenile platypuses indicated dispersal and/or higher mortality than in adult animals. However, in the upper Shoalhaven River study, 51–60% of adults individuals were not recaptured (Grant 1992*b*), and unmarked adult animals were still being captured after a total of 346 had been marked and released in the study area, which consisted of 16 pools along 12.5 km of the Shoalhaven River and 3.9 km of an adjacent creek (Grant 1992*b*). Goldney (1996) found transience and site attachment in some platypuses in his study area in the Duckmaloi River, near Bathurst in New South Wales, and failed to recapture a high proportion of both juvenile and adult platypuses within two years of their first capture. The notion of resident and transient animals within the population was given some support by the preliminary genetic profiling work of Gemmell (1994). More recent work being carried out on DNA markers from this population, including microsatellite loci and mitochondrial DNA (mDNA), has also detected allelic frequency differences between sub-populations within the upper Shoalhaven River study area, which are consistent with observations on mDNA genotypes (Gemmell 1994; Akiyama *et al*. 1996). Allelic frequency differences have also been found between populations of platypuses from different streams, suggesting continuous geographical gradation, consistent with an isolation-by-distance geographical structure (Akiyama *et al*. 1996).

A clear and detailed understanding of the population structure, juvenile dispersal and the mating system of the platypus is essential for the development of conservation and management strategies. It is also important for assessing the potential impact of developments that affect riparian and riverine habitats. These aspects of platypus field biology have remained the most elusive because of the secretive nature of the nocturnal, diving and fossorial habits of the species. Improvements in remote sensing technology and developments in molecular biology will eventually provide essential insights into the nature of the social organization of the platypus.

8. CONCLUSION

Recent research into the ecology and field biology of the platypus has covered much of the ground previously trodden by many of the early expatriate biologists and naturalists in the field, and similar conclusions were reached in many instances. This, however, does not represent a waste of time and effort, as the lack of quantitative information presented by the early workers meant that substantiation was often necessary. During this process of substantiation, further valuable information on aspects of the biology of platypuses has often been obtained. Some observations made by the early naturalists have not stood up to more critical assessment and have been rejected. In a paper presented at a conference hosted by the Smithsonian Institution in Washington, Grant (1983*a*) stated that 'current research on the behavioural ecology of the three extant species of the order Monotremata has been mainly concerned with answering fairly simple questions about the natural history [of the species]'. That statement made over a decade ago is no longer true for studies of either behaviour or ecology of the platypus today. At the National Symposium on Platypus Biology held at Charles Sturt University, Bathurst, New South Wales, in November 1996, 26 papers reporting investigations of the field biology of *O. anatinus* in several states of Australia were presented. These papers included work using technologies such as molecular biology, radio-tracking and radio-telemetry, geographic information systems, assessment of field metabolism using the doubly-labelled water technique and the use of a variety of sophisticated statistical procedures, which could not have been imagined by the first expatriate biologists and early naturalists. Although some of the workers involved in these studies presented only preliminary information of on-going work, the findings of others (including those referred to in the above review) are published in volume 20 of *Australian Mammalogy* (1998).

Since Europeans first recorded and described the animal almost exactly 200 years ago (Hunter (1798), cited in Home (1802)), a great deal has been learned regarding the field biology of *Ornithorhynchus anatinus*. However, as discussed in this review, much is still to be learnt about this unique Australian species—a species described by Merv Griffiths, one of the foremost authorities on its biology, as 'the animal of all time'.

The authors express their appreciation to Merv Griffiths, Gina Grant, Meredith Temple-Smith and to the many friends and colleagues who provided field assistance, discussion and encouragement during their studies of the platypus. The authors thank Merv Griffiths for providing a number of the historical references, Sue Simpson for preparing the diagrams, and David Goldney for his unpublished information on the movements of platypus past the Duckmaloi Weir.

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