



FAUNA *of* AUSTRALIA



17. NATURAL HISTORY OF THE CHELONIA

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LIFE HISTORY

Females of all species of turtle (except perhaps *Chelodina rugosa*, see below) leave the water to deposit their eggs in cavities or depressions constructed in the surrounding sand, soil or litter. Turtles abandon the eggs once they are laid and do not protect the hatchlings. All species have distinct annual breeding seasons. Synchronisation of breeding with periods of ample food availability is unnecessary, because turtles can accumulate resources over time to provide for the demands of vitellogenesis (Chessman 1978; Georges 1983; Kuchling & DeJose 1989). This ability is carried to extremes in marine species, with *Chelonia mydas* taking in excess of one year to prepare for a breeding season (Limpus & Nicholls 1988). Nor is there a need for breeding to coincide with conditions suitable for copulation, as the male and female cycles are not particularly closely synchronised in chelonians. Males of most Australian species have sperm in the epididymides in all months, and females of some species overseas have been found to store sperm for several years.

There are three principal constraints on the reproductive patterns of chelonians. Firstly, females must nest when conditions are conducive to adult activity. They must also nest when the conditions to follow are conducive to embryo survival and ultimately, embryonic development. Thirdly, they must ensure that the hatchlings emerge when conditions are conducive to their survival. Knowledge of each of these constraints in the context of the ecology of a species is generally sufficient to explain its reproductive strategy.

A plethora of solutions for meeting these constraints has evolved. There is variation among species and plasticity among populations of the same species in the timing of egg laying, clutch size, clutch frequency and incubation period. Effective incubation may be prolonged by cold torpor arrest during the winter months, embryonic diapause, delayed hatching, embryonic aestivation, and delayed emergence from the nest after hatching (Ewert 1985).

Reproductive Patterns for Freshwater Turtles

Two broad reproductive patterns can be identified among Australian freshwater turtles—one temperate and one tropical—though whether there is an overriding taxonomic influence on these patterns is debatable (Legler 1985; Kuchling 1988).

Winter provides a major interruption to adult activity and growth, and an impediment to embryonic development, for turtles of the temperate zones. *Emydura krefftii* from Fraser Island in Queensland exhibits a typical reproductive pattern for temperate-zone turtles of both the northern and southern hemispheres (Georges 1983). Mating occurs all year round with peaks in the autumn and spring. Sperm are present in the epididymides of males all year round, but spermatogenesis is post-nuptial with a peak in testicular activity in autumn and a cessation of testicular activity during the breeding season. Yolk begins to accumulate in the ovaries of females in late summer and continues through winter, presumably by a transfer of material from fat stores to the ovaries. Ovulations and nesting begin in early spring. Up to three clutches are laid by each female between early spring and mid summer. Clutch size ranges from four to ten eggs, depending upon the size of the female. Hatchlings emerge from nests in mid to late summer and make their way to the water. There is ample time for incubation and hatching to occur before the onset of winter.

Although it is the most prevalent pattern, spring nesting and summer hatching is not universal among Australian freshwater turtles, even within the temperate zones (see Chapter 21). For example, *Chelodina oblonga* nests in the spring, early summer and mid summer. *Pseudemydura umbrina* nests in the spring. In

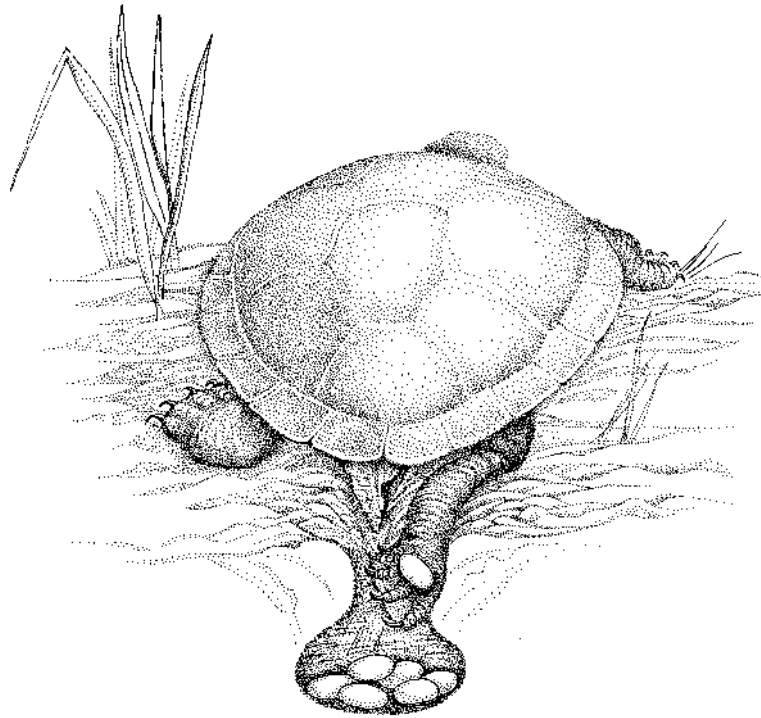


Figure 17.1 Egg laying in the chelid *Emydura macquarii* [T. Wright]

both species, hatching is initiated by winter rains (Burbidge 1981; Clay 1981). *Chelodina expansa* nests in the autumn and winter (Goode & Russell 1968; Georges 1984; Legler 1985).

Tropical freshwater species are freed from the constraints of reduced winter temperatures, and show the greatest diversity in reproductive patterns. Rainfall throughout the Australian tropics is markedly seasonal (Taylor & Tulloch 1985). There is typically a dramatic rise in water levels in the monsoonal wet season (December to March) and a corresponding drop in water levels in the wet-dry transitional months (April, May) and the following dry season (June to August). Freshwater species inhabiting the tropics often have only a very short period in which to find the relatively dry ground suitable for nesting, and they have solved the problem in a variety of ways. *Chelodina rugosa* lays eggs underwater or in saturated soils (Kennett, Christian & Pritchard 1993a). If local conditions have dried, *C. novaeguinea* may move to more permanent water bodies or aestivate until conditions are appropriate (Covacevich, Couper, McDonald & Trigger 1990a; Kennett, Georges, Thomas & Georges 1992) (see Chapter 21).

Tropical *Emydura* spp. inhabit permanent water and, unconstrained by seasonal disappearance of water, they nest at the same time as their southern counterparts. Their eggs incubate and hatch during the northern dry-season. Pig-nosed turtles, *Carettochelys insculpta*, also inhabit permanent water, and nest between late August and mid November (Webb *et al.* 1986; Georges & Kennett 1989).

After about 65 to 70 days of incubation, and rapid development for eggs of their size, *Carettochelys* embryos are at a final stage of development and are quite capable of hatching. Instead, they enter a form of embryonic aestivation. Their metabolic rate and demand for oxygen drops precipitously (Webb *et al.* 1986) and they wait for an appropriate stimulus before hatching. Webb *et al.* (1986) showed that immersion in water was sufficient to arouse the torpid offspring and hatching followed. In the field, both flooding and torrential rain can stimulate hatching (Fig. 22.2; Georges 1987).

Clearly, hatching of the young turtles is delayed until the first heavy rains of the wet season flood the nests or saturate the surrounding sands. Presumably the hatchlings gain some benefit from this strategy, hatching into water where there may have been none before, and the rain may have opened up new areas into which the hatchlings can disperse to feed and seek shelter. Hatching in response to a discrete stimulus may ensure synchronised hatching and so help to overcome variation in development rates caused by thermal gradients in nests (Georges 1992; Thompson 1986). predators may be satiated as a result of simultaneous hatching of all nests on a nesting bank (Carr 1967), and the floodwaters responsible for hatching may have dispersed potential predators previously concentrated in the contracted waterbodies.

Reproductive Patterns for Marine Turtles

Marine turtle eggs require nest temperatures between 25° to 33°C and a nest in a low salinity, well-ventilated substrate with high humidity, placed where it has a low probability of being flooded or eroded (Miller 1985; Maloney, Darian-Smith, Takahashi & Limpus 1990). These conditions can be met above the storm surge level on most tropical or subtropical beaches protected from strong wave action by headlands or intertidal reef flats. Nesting is distinctly seasonal and restricted to the summer months on subtropical beaches (Limpus 1971a). Closer to the equator, the period of suitable temperatures is longer and some beaches may be suitable for successful incubation all year round (Limpus, Miller, Baker & McLachlan 1983a). The success of a rookery depends upon environmental parameters, such as beach stability, the seasonal mosaic of nest temperatures that determine hatching success and hatching sex ratio, and the proximity of offshore currents for dispersal of hatchlings to suitable oceanic feeding areas.

With the onset of the breeding season, adult males and females migrate from feeding grounds to copulate near the nesting area (Limpus, Miller, Parmenter, Reimer, McLachlan *et al.* 1992; Limpus, Parmenter, Baker & Fleay 1983c; Parmenter 1983). There is no pair bond between individuals and copulation with a number of different partners during the mating season is normal (Fig. 19.3; Limpus 1993; Harry & Briscoe 1988). The female stores the sperm from her several mates for use later in the breeding season. At the completion of mating

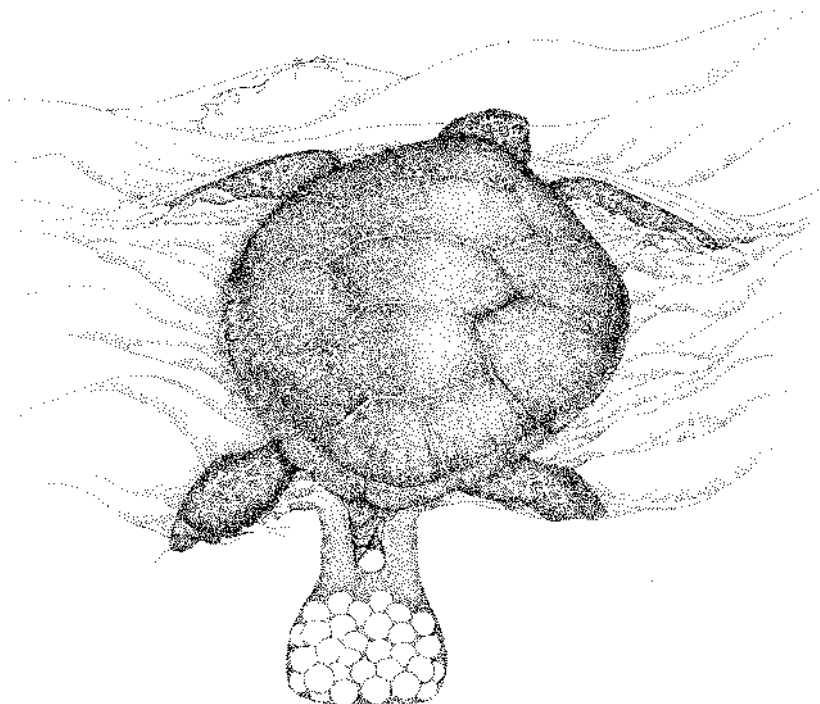


Figure 17.2 Egg laying in the cheloniid, *Chelonia mydas*[T. Wright]

the males depart, presumably returning to the distant feeding grounds (Limpus 1993). Each female moves to an area adjacent to her selected nesting beach and commences production of eggs, fertilising them from her sperm store. Because of the mixture of sperm she carries, several males usually contribute to the fertilisation of any one clutch (Harry & Briscoe 1988). The female comes ashore to nest, usually at night, several weeks after her first mating. For those beaches fronted by reef flats, nesting coincides with the higher tides.

Within the one nesting season, each female typically lays several clutches at about two weekly intervals (Hirth 1980; Limpus 1985; Limpus, Fleay & Baker 1984a; Limpus, Fleay & Guinea 1984b). Between clutches the female moves just offshore from the nesting beach to make the next clutch of eggs, again fertilising them from stored sperm. Breeding turtles do not feed, or else feed to only a limited extent, while migrating, courting or making eggs at the nesting beach area. They live on the fat reserves deposited before the breeding season.

The number of eggs and egg size varies among species. *Natator depressus* lays about 50 billiard-ball size eggs per clutch and three clutches per breeding season (Limpus 1971a; Limpus *et al.* 1984a). *Eretmochelys imbricata* lays about 132 ping pong ball-sized eggs per clutch in about three clutches per season, while *Chelonia mydas* lays about 115 intermediate-sized eggs per clutch and about six clutches per breeding season (Limpus, Parmenter, Baker & Fleay 1983d). Females lay their eggs high up on the beach usually within the vegetated strand. Miller (1985) has described the embryology of marine turtles. Eggs hatch at about 6–13 weeks after laying, depending on incubation temperature, as described further in Chapter 19.

Females usually return to the same beach or island to lay several clutches within the one nesting season. However, a small percentage will lay on more than one beach within a few hundred kilometres of the initial nesting site (Limpus *et al.* 1984a, 1984b). At the completion of the nesting season the female returns to the same feeding ground that she left at the start of her breeding migration (Fig. 19.3; Limpus *et al.* 1992). Individual females breed every 2 to 8 years, generally returning to nest on the same beach (Limpus 1985; Limpus *et al.* 1984a, 1984b). This behaviour, and the annual use of traditional nesting beaches, has led to the assumption that a marine turtle returns to nest on the precise beach of her birth. In reality, the homing is probably not so exact. Genetic studies suggest that the female returns to breed in the general region of her birth (Bowen, Kamezaki, Limpus, Hughes, Maylan *et al.* in press; Norman, Moritz, Limpus & Prince in press; Gyuris & Limpus 1988).

Sex Determination

Sexual differentiation of the embryo is profoundly influenced by incubation temperature in many marine, freshwater and terrestrial turtles (reviewed by Bull 1980, 1983; Ewert & Nelson 1991). For most species, females are produced at high temperatures and males at low temperatures. A very narrow range of temperatures, referred to as the threshold or pivotal temperature, produces both males and females (Bull 1983). A few species have upper and lower thresholds, and females are produced at the extremes of temperature (Yntema 1976; Gutzke & Paukstis 1984). Sex determination is not temperature dependent in those Australian chelids studied to date (Bull, Legler & Vogt 1985; Georges 1988a; Thompson 1988; Palmer-Allen, Beynon & Georges 1991), whereas *Carettochelys insculpta* (Webb *et al.* 1986; Georges 1992) and all marine species (Limpus & Miller 1980; Limpus, Reed & Miller 1985) have the trait.

Eggs of *Carettochelys insculpta* incubated at a constant 32°C, or hotter, produce 100% females whereas those incubated at 30°C or cooler produce 100% males (Webb *et al.* 1986). In the field, hot exposed nests produce females, cool shaded nests produce males, and nests intermediate in temperature produce hatchlings

of both sexes (Georges 1992). In nests that produce hatchlings of both sexes, males tend to emerge from the deepest, coolest eggs and females tend to emerge from the uppermost, hottest eggs. The ecological significance of temperature dependent sex determination is obscure.

Sex determination in marine species has been better studied. Females spread their nesting over a series of beaches which encompass a range of nest temperatures either side of the pivotal temperature, the theoretical temperature that should produce a 1:1 sex ratio (Limpus, Reed & Miller 1983b). As a result, the sex ratio for each species, or breeding stock, depends on the proportion of clutches laid in each of these warm and cool nesting areas. Cyclones, with their associated high rainfall and cooling effect on the beaches, can modify the general seasonal trend in hatchling sex ratio from a rookery. A cyclone can cause short-term cooling events with up to 5°C drops in nest temperature over a few days. Should this happen at mid-incubation, clutches can contain all males, while clutches emerging a few days earlier or later than these may contain all female hatchlings (Reed 1980).

Growth and Demography

The order Chelonia includes some of the most fecund amniotes on earth. Estimates of reproductive potential range from 4.4 for the chelid, *Pseudemydura umbrina*, to 690 per year for the cheloniid, *Chelonia mydas*. Typically, there is a strong positive relationship between clutch size and maternal body size (Georges 1983; Miller 1989); reproductive potential in these species may increase with age.

High fecundity is matched by vulnerability of the egg and hatchling stage to predation. Parmenter (1985) estimated that in the absence of predation, survivorship of *Chelodina longicollis* eggs at Laurendale near Armidale was 72%, but predation reduced this figure to 37%. Predation in the study areas was estimated to be much higher, and close to 100%. Predators included the European Red Fox, *Vulpes vulpes* and domestic cat, *Felis catus*. Water rats, goannas and crows exacted a high toll on nests of *Emydura macquarii* in South Australia, and foxes alone preyed on an estimated 93% of nests (Thompson 1983). In contrast, nest predation is rare among *Emydura* sp. on Cooper Creek in central Australia (Thompson 1983) where foxes are rare. Juvenile turtles probably fare much better in the water. Gibbons (1968) reported that the chance of survival of hatchlings in the North American species, *Chrysemys picta*, was very high, although only 2% of the eggs survived to hatch. There are no useful data for post-hatching survival in Australian species.

There are few direct estimates of recruitment to freshwater turtle populations in Australia, but it can be reasonably assumed that the populations are sustained by a trickle of new recruits, or by successful recruitment in the few years when conditions allow many nests to survive to hatching. The longevity of adults is necessary for populations to be sustained by such low or intermittent recruitment.

The difficulties of studying growth in a long-lived slow growing vertebrate have discouraged research on this topic in Australia, and few relevant studies have been published. In the temperate zones, freshwater turtles have an annual cycle of growth, even at latitudes that permit activity and feeding in all months (Georges 1982a). Growth of *Emydura krefftii* (Fraser Island) is poorly correlated with body size, so it is not possible to calculate a satisfactory relationship between age and size. In general, juveniles of all species so far studied grow faster than adults, and growth rate drops abruptly at the onset of maturity, when available resources are redirected to reproduction (Georges 1985). Females of *Emydura* and *Chelodina* species tend to grow faster than males and to reach

larger maximum sizes (Parmenter 1976; Chessman 1978; Georges 1982a). *Pseudemydura umbrina* is the only species in which the males grow to larger sizes than females (Burbidge 1981).

Onset of maturity typically occurs between seven and 12 years of age (Burbidge 1981; Georges 1982a; Parmenter 1985). Females tend to mature at larger sizes than males. There are no data on longevity for any Australian turtle, although Georges (1982a) estimated that if a specimen of *Emydura krefftii* (Fraser Island) grew at the fastest observed rate of any turtle in its size cohort, it would take at least 69 years to reach maximum size.

There are relatively few estimates of population densities of freshwater turtles in Australia. *Chelodina longicollis* is very abundant in the permanent dune lakes of the Jervis Bay Territory (up to 163.8 ± 34.2 turtles/ha; 9.9 ± 2.1 per 10 km of shoreline; Georges, Norris & Wensing 1986), and in lentic waters of the New England Tableland (up to 400/ha in farm dams; Parmenter 1976). Density estimates for *Chelodina longicollis* from Gippsland ranged from 160 turtles/ha for lagoons and 240 turtles/ha in farm dams, equivalent in both instances to about 70 kg/ha (Chessman 1978). Population densities for *Carettochelys insculpta* in the upper reaches of the South Alligator River have been estimated at 33.8 ± 11.3 turtles/ha (equivalent to 67 turtles/km of channel or 227.4 kg/ha) (Georges & Kennett 1989). These estimates are high in comparison with estimates for species of freshwater turtles on other continents (Iverson 1982; Congdon, Greene & Gibbons 1986). However, in each of these studies, the turtle densities were probably inflated above the carrying capacity of the waters in which they were found because of seasonal contractions of their aquatic habitat (Georges & Kennett 1989; Kennett & Georges 1990).

An estimate of sustainable density is available for *Emydura krefftii* on Fraser Island. In Lake Coomboo, they have a population density of 87 turtles/ha, equivalent to 28.8 ± 0.7 kg/ha. Biomass production was 18.5 ± 3.4 kg/ha (Georges & Legler in press).

The population structure of freshwater turtle populations is highly variable, presumably dependent upon recent history of recruitment. Generally adults predominate or are present in equal numbers to juveniles (Georges 1985), but age structures have not been determined for any Australian species. Sex ratios are typically close to 1:1 for chelid turtles, which have genotypic sex determination, but skewed in favour of females for *Carettochelys insculpta* which has environmental sex determination (Georges 1988a).

Most marine turtle eggs are laid on islands where potential egg predators are scarce. The principal threats to egg survival in Australia are early infertility and/or embryonic death, flooding and erosion, and possibly microbial invasion (Parmenter 1980; Limpus 1985; Limpus *et al.* 1983a, 1983d, 1983b). At most rookeries, approximately 60 to 80% of eggs can be expected to produce hatchlings which reach the beach surface. Exceptions are the eggs of *Caretta caretta*, which are subject to predation by *Vulpes vulpes* on the mainland north of Bundaberg, and those of *Natator depressus* which are eaten by pigs (*Sus* sp.) and varanids on the mainland south of Bamaga and in the Northern Territory. At most rookeries, there is <2% loss of hatchlings to terrestrial predators during the beach crossing (Limpus 1973), unless nocturnal predators are present (Limpus *et al.* 1983d).

The most intense predation on hatchlings probably occurs in the sea, however recruitment and survivorship in feeding areas are poorly documented. The principal predators of large marine turtles are tiger sharks, crocodiles, toothed whales and man (Balazs 1980; Limpus *et al.* 1983d; Caldwell & Caldwell 1969). Survivorship from egg to breeding adult is low, estimated at between a few per thousand and a few per ten thousand for *C. caretta* (Limpus 1985; Frazer 1986). Marine turtles in Australia display slow growth and are decades

old at first breeding; for example >30 years for *C. mydas*, *C. caretta* and *E. imbricata* in the southern Great Barrier Reef (Limpus & Walter 1980; Limpus 1985, 1992a). Because of the long period before sexual maturity, survivorship of large immature and adult marine turtles must be very high and the adult must have a long breeding life to maintain population stability (Crouse, Crowder & Caswell 1987). Consequently marine turtle populations consist of a large proportion of immature turtles (Limpus & Reed 1985a; Limpus 1985, 1992a). These same studies have identified widely varying sex ratios for *C. mydas*, *C. caretta* and *E. imbricata* inhabiting the southern Great Barrier Reef. Of these species *E. imbricata* occurs at the lowest density (3.34 turtles/km², and with a low biomass (0.82 kg/ha) (Limpus 1992a).

ECOLOGY

Diet

Turtles, with their rounded body form and heavy investment in bony skeletal elements, are not renowned for their agility, and this has placed restrictions on the foods they can exploit (Pritchard 1984). Most freshwater turtles are omnivorous, although some species have resorted to herbivory (for example, testudinids), and there are a few carnivorous specialists, such as *Pseudemys umbrina*, *Chelus* species from South America and *Claudius* species from Mexico. Carnivorous turtles may feed upon invertebrate prey even slower than themselves, while others rely upon stealth to secure more mobile prey.

Australian freshwater turtles typically are omnivorous (Fig. 17.3; Chapter 21). Temperate species of *Emydura*, for example, consume a broad range of foods including filamentous algae, periphyton (including sponges), a wide variety of aquatic macrophytes, aquatic macroinvertebrates, terrestrial insects which fall or are blown onto the water, and carrion (Legler 1976; Georges 1982b; Chessman 1986). There is a general tendency for juveniles of omnivorous species to be more carnivorous than adults (Fig. 17.3; Georges 1982b; Moll & Legler 1971).

Omnivorous species of the wet-dry tropics, such as *Carettochelys insculpta*, *Elseya dentata*, *Emydura victoriae* and *Emydura 'australis'*, rely heavily upon the seeds, fruits and leaves of riparian vegetation during the dry season, supplemented with aquatic macrophytes, algae, macroinvertebrates and carrion (Fig. 17.3; Legler 1976; Georges & Kennett 1989).

There is considerable overlap, especially among omnivorous species, in the dry season habitat preferences and diets of the tropical turtles. It may be that these similarities do not persist during the wet season, and that unique aspects of habitat and food preferences among species would emerge if studies were conducted then. Alternatively, the highly variable nature of the tropical climate, and the interconnectedness of aquatic environments in wet seasons, may result in interchange and re-invasion of river systems by ecologically similar species, at a greater rate than the slow process of competitive exclusion.

Newly hatched marine turtles presumably feed on the macroplanktonic algae and/or animals in surface waters. Juvenile marine turtles, except *Dermochelys coriacea*, are principally benthic feeders during residence in shallow waters of the continental shelf. *Dermochelys coriacea* is a plankton feeder throughout life, feeding principally on jellyfish and planktonic tunicates (Brongersma 1972). In Australian waters, *C. mydas* feeds mostly on seaweed, seagrass and mangrove fruits, *C. caretta* and *Lepidochelys olivacea* feed mostly on shellfish and crabs, *N. depressus* feeds mostly on soft corals and sea pens, and *E. imbricata* eats sponges primarily. All species eat jellyfish and Portuguese man-of-war on occasions (Lanyon, Limpus & Marsh 1989; Moody 1979; Guinea & Limpus unpub. data).

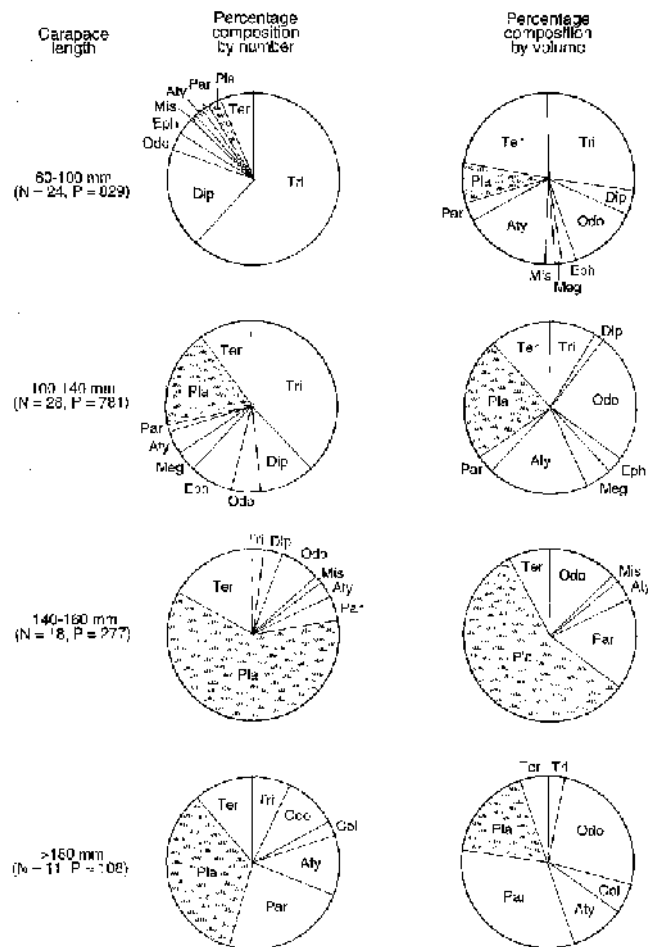


Figure 17.3 Variation in the composition of the diet of *Emydura krefftii* with increasing body size, as measured by the frequency of occurrence of prey in stomachs by number or by volume. **aty**, atyid crustaceans; **col**, coleopteran larvae; **dip**, dipteran larvae and pupae; **eph**, ephemeropteran nymphs; **meg**, megalopteran larvae; **mis**, miscellaneous aquatic insects; **odo**, odonate nymphs; **par**, parastacid crustaceans; **pla**, plant material; **ter**, terrestrial arthropods; **tri**, trichopteran larvae [W. Mumford]

Patterns of Habitat Use

Chelonians have specialised along two major paths with respect to habitat utilisation. Marine turtles of both the Cheloniidae and Dermochelyidae migrate as adults (Meylan 1982) and have a planktonic dispersal phase as young (Carr 1986). Such highly mobile animals can utilise widely separated habitats, enabling them to optimise feeding and survival for different age/size classes and select specialised breeding habitats. This is made possible by the relative stability and predictability of the marine ecosystem.

In freshwater and brackish water ecosystems the habitat is fragmented and a turtle will require wider physiological and morphological capabilities if it is to disperse widely as it will have to traverse terrestrial or marine habitats. In reality, these capabilities are limited. As a result, freshwater and brackish-water turtles tend to be restricted to particular river systems. Consequently, their lifestyle needs to be more closely adapted to deal with the vagaries of local climate and ecology.

Many species of Australian freshwater turtle occupy only permanent water of riverine and lentic ecosystems. Often several species will co-occur in the one river drainage. For example, six species of freshwater turtle occur in the Fitzroy-Dawson drainage of Queensland (Legler & Cann 1980). The dominance of each

in different microhabitats, as described in Chapter 21, together with variation in diet, presumably allow these species to co-exist in the same drainage. In discussing similar patterns of habitat fidelity on Fraser Island, Georges, Norris & Wensing (1986) speculated that the combined presence of *Emydura krefftii* and *Chelodina expansa* in the permanent dune lakes might virtually exclude *C. longicollis* because of competition for food. Such competition may be exacerbated by the presence of fish (Chessman 1988).

Competition between species is remarkably difficult to demonstrate, primarily because the effects of passive competitive exclusion and character displacement are most evident at evolutionary time scales. Theories of passive competition for resources that explain the distribution and abundance of freshwater turtles in Australia have very little direct experimental support and remain speculative.

Ephemeral aquatic environments are generally highly productive, particularly if they have dried completely before refilling. In addition, species that would otherwise compete with turtles for food, such as fish (Chessman 1984), are often unable to invade isolated ephemeral swamps. However, the numerous species of freshwater turtle that do exploit the benefits of such environments are still subject to the problem of periodic and often unpredictable habitat loss. Many species aestivate during such dry periods, including *Pseudemydura umbrina*, *Chelodina rugosa*, *C. steindachneri* and *C. novaeguineae*. *Chelodina longicollis* migrates to more permanent water.

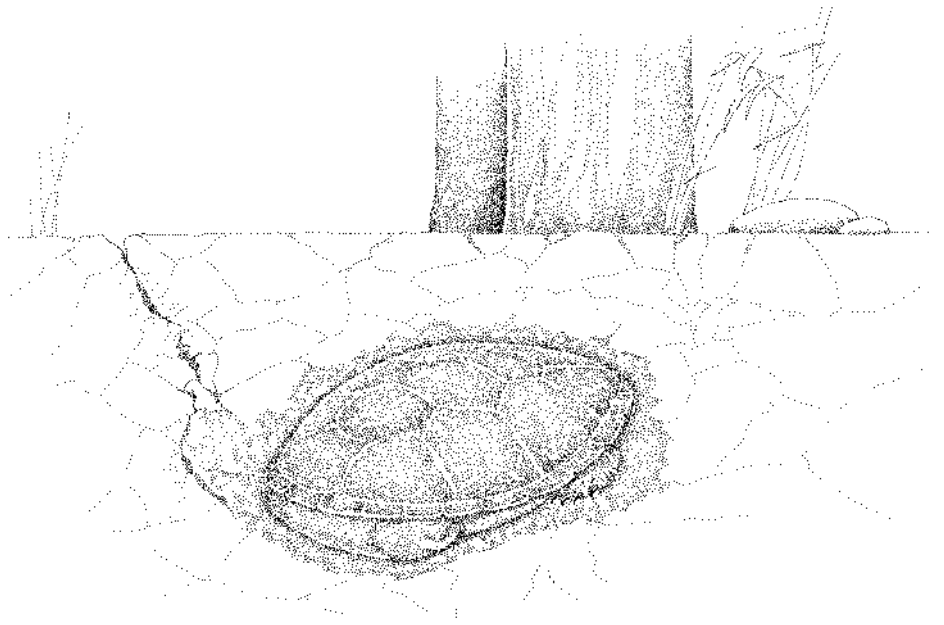


Figure 17.4 Position and posture of the chelid *Chelodina rugosa* during aestivation [T. Wright]

In southern New South Wales, *Chelodina longicollis* migrates overland to seek refuge in permanent dune lakes when ephemeral swamps and ponds dry during periods of low rainfall. At such times, the number of turtles in the lakes reflects the carrying capacity of both the permanent and ephemeral waters of the region, and may well exceed the carrying capacity of the lakes alone. Exceptionally high population densities were recorded for these lakes at the end of 1978–1983 drought (Georges *et al.* 1986). As a result, turtles were in poor body condition, grew slowly and failed to breed in 1986 (Kennett & Georges 1990).

Following a drought, *Chelodina longicollis* returns to the ephemeral waters as they become available again, and act as the focus for reproduction, recruitment and growth. Rain appears to stimulate a very rapid migratory response in this

species. The migratory tendencies of *C. longicollis* probably first evolved in response to selection for an ability to exploit productive ephemeral waters in the absence of competition from fish (Chessman 1984) and other species of turtle (Georges *et al.* 1986; Chessman 1988). Once populations grew to approach the carrying capacity of both the ephemeral and permanent waters of a region, individuals would have often found themselves occupying more restricted permanent water during extended dry periods, where intense intraspecific competition for food would cause a sharp decline in growth and reproductive output, as described above. In turn this would enhance selection for a rapid migratory response and preference for ephemeral habitats.

Reproductive potential and onset of sexual maturity depend on size and not age in turtles (Gibbons 1982), so any delay in growth while occupying a drought refuge would have considerable consequences for reproduction of individuals. Under these circumstances, occupation of ephemeral waters would afford much greater selective advantages than could have been predicted from a comparison of production in ephemeral and permanent waters alone.

In the tropics, *Chelodina rugosa* and *C. novaeguineae* attain highest densities in ephemeral waters. They take advantage of high production during the wet season and survive the dry season by migrating to permanent water or by aestivation. *Chelodina rugosa* occupies shallow ephemeral waterbodies of floodplains in low lying country adjacent to the Gulf of Carpentaria and between the Arnhem Land and Kimberley plateaux. At the end of the dry season, *C. rugosa* buries beneath the mud of the waterbody in which it lives, to await the wet season inundation. It obtains its oxygen through a breathing hole until the ground dries and cracks. This cycle of aestivation and activity of *C. rugosa* is annual.

Chelodina novaeguineae occupies more marginal xeric environments where annual rainfall is less predictable. When the ephemeral waterbodies dry, individuals migrate to the surrounding scrub and aestivate beneath litter, in the burrows of other animals or in drainage crevasses. Aestivation by *C. novaeguineae* is not necessarily annual, and the species can aestivate for two or more years (Cann pers. comm.).

Marine turtles utilise traditional nesting beaches in tropical and warm temperate regions and feed throughout the tropical and temperate seas of the world at some stage in their life cycles. *Dermochelys coriacea* migrates to tropical nesting beaches from open ocean feeding grounds as far afield as the high latitude waters adjacent to pack ice (Pritchard 1971; Goff & Lien 1988). Along Australian shores, *D. coriacea* nests infrequently in south-eastern Queensland, but it is commonly encountered feeding along the continental shelf to the south of the Great Barrier Reef and off south-western Western Australia (Limpus & McLachlan 1979).

Natator depressus nests only on continental islands and the mainland coast of Australia, largely avoiding beaches fringed by coral reef (Limpus, Gyurus & Miller 1988; Parmenter in press). Unlike other marine turtles, post-hatchling dispersal does not include an oceanic component and this species spends most of its life over the Australian continental shelf (Walker & Parmenter 1990). The species is captured most frequently over soft bottom inshore habitats of the Great Barrier Reef, within the Gulf of Carpentaria and throughout the Arafura Sea (Limpus *et al.* 1983c; Poiner & Harris in press).

The remaining marine turtle species have an oceanic post-hatchling dispersal phase in the life cycle (Fig. 19.4; Carr 1986). In Australian waters, *Chelonia mydas* nests principally on islands near the oceanic margin of the continental shelf, from the tropics northwards. *Eretmochelys imbricata* nests on islands on the inner margin of the Continental shelf within the tropics, and *Lepidochelys*

olivacea nests principally on continental islands in north western Arnhem Land. *Caretta caretta* nests on the mainland and adjacent islands near the Tropic of Capricorn on both the east and west coasts (Limpus 1982, unpub. data).

The adult and immature turtles of these species occupy a diversity of feeding areas within a radius of some 2600 km of their rookeries (Limpus *et al.* 1992). *Chelonia mydas* feeds principally in coral reef and inshore seagrass pastures in tropical and warm temperate areas (Lanyon *et al.* 1989). *Eretmochelys imbricata* is most commonly found feeding in coral and rocky reef habitats in tropical areas (Limpus 1992a; unpub. data), while *Lepidochelys olivacea* feeds over soft bottomed habitats across northern Australia (Harris in press; Poiner & Harris in press). *Caretta caretta* feeds across a diversity of habitats including shallow coral reefs to deeper soft bottomed habitats of the continental shelf along all but the southern coast of Australia, although it may be most abundant in warm temperate habitats (Limpus unpub. data).

BEHAVIOUR

Mating

Mating behaviour in turtles has been little studied. In freshwater species, mating behaviour appears to vary between species (Murphy & Lamoreaux 1978), though cloacal touching precedes mounting in all species studied, as described in Chapter 21. In marine species, the males and females aggregate for mating in the vicinity of the nesting beach (Limpus 1993). The male mounts on top of the female, using all four flippers, and enlarged claws in cheloniid turtles, to grasp the carapace of the female. He then curls his elongate tail under the female to bring the cloacae together, allowing for insertion of the penis (Booth & Peters 1972; Bustard 1972). Although a pair may be joined for many hours, copulation may occur for a much shorter time.

Nesting

Typically, many freshwater turtles undertake nesting activity at night, triggered by rain that falls during the breeding season (Goode 1967; Vestjens 1969). Water temperatures appear important for other species, such as *Carettochelys insculpta*, (Georges unpub. data) and a period of starvation followed by a flush of food availability is an important factor in the successful ovulation and nesting of *Pseudemydura umbrina* (Kuchling & DeJose 1989).

Nesting behaviour has been observed for a number of Australian chelids. After digging a cavity, *Emydura macquarii* deposits its eggs, fills the excavation with soil, and then drops its shell hard onto the ground to compact the soil in the filled nest (Goode 1965; see also Chapter 21). This tamping of the soil has been observed also in *Chelodina longicollis* (Vestjens 1969), *Chelodina oblonga* (Clay 1981), *Chelodina expansa* (Georges pers. obs.) and *Pseudemydura umbrina* (Kuchling in press).

The nesting behaviour of all marine turtle species is very similar (Bustard & Greenham 1969; Bustard, Greenham & Limpus 1971). The female searches out a nest site above the high tide level and excavates a depression (body pit) of variable depth, using all four flippers, and places her body down to the level of relatively firm sand. She then excavates a vertical, flask shaped egg chamber under the tail using the hind flippers. The eggs are laid such that they drop directly into the egg chamber. At the completion of laying, moist sand is scooped into the chamber with the hind flippers, and tamped down at intervals as the chamber fills. The tamping action of smaller species (*L. olivacea*, *E. imbricata*, *N. depressus*) may be quite vigorous. When the egg chamber is filled, the female then digs her way forward for a variable distance, using her front

flippers to dig sand from the front and fling it back, and the hind flippers to push sand to the middle back of the body pit. After the pit is refilled, the female returns directly to the sea. The duration of nesting varies from about an hour (*L. olivacea*, *E. imbricata*, *N. depressus*), to one and a half hours in *C. caretta* and *D. coriacea*, and three hours in *C. mydas*.

Following pipping, the hatchling remains for a day or so at the egg shell while it uncurls and internalises the remains of the yolksac (Miller 1985). The hatchlings dig as a group to the surface over several days and emerge from the nest, usually at night (Bustard 1967b; Limpus 1973, 1985). On emergence, they orientate to low elevation light horizons (Limpus 1971b; Salmon, Wyneken, Fritz & Lucas 1992) which will normally direct them seawards. There is evidence of imprinting of the hatchlings to the earth's magnetic field at the nest (Lohmann 1991), and possibly to the water that they first contact (Grassman, Owens, McVey & Marquez 1984). Immediately the hatchlings reach the water they begin swimming, and orientate perpendicular to wave fronts, a behaviour which normally takes them into deeper water (Salmon & Lohmann 1989). The hatchlings at this stage live on yolk from the yolksac and do not feed or sleep while on the beach or while swimming out to sea.

Thermoregulatory behaviour

Chelonians, like all reptiles, are ectothermic. They rely upon ambient temperatures remaining within the range conducive to their general activity, or when this is not so, the animals use thermal sources and sinks within their environment to maintain body temperatures within the preferred range. Reptiles have a vast repertoire of behaviours to regulate their body temperatures within fairly narrow limits while active, quite irrespective of ambient temperatures, but turtles are limited in this regard because the water in which they live is thermally conductive and they lack effective insulation. While large turtles can be expected to have considerable thermal inertia, and circulatory mechanisms exist to minimise heat transport from body core to the surface (Hutchison 1979), for most freshwater turtles, any elevation in body temperature achieved is quickly dissipated in the surrounding water.

Freshwater turtles thermoregulate primarily by seeking out warmer strata, typically at the water surface or in slower moving shallow waters, by basking in the sun's rays while floating at the surface, or by leaving the water altogether and basking (Fig. 17.6; Chapter 21). Basking is a major component of daily activity in Australian chelids (Webb 1978), and occurs in two major periods for *Emydura* sp. and *Elseya latisternum*. These shortnecked chelids bask until they exhibit signs of discomfort similar to those reported in the Panamanian

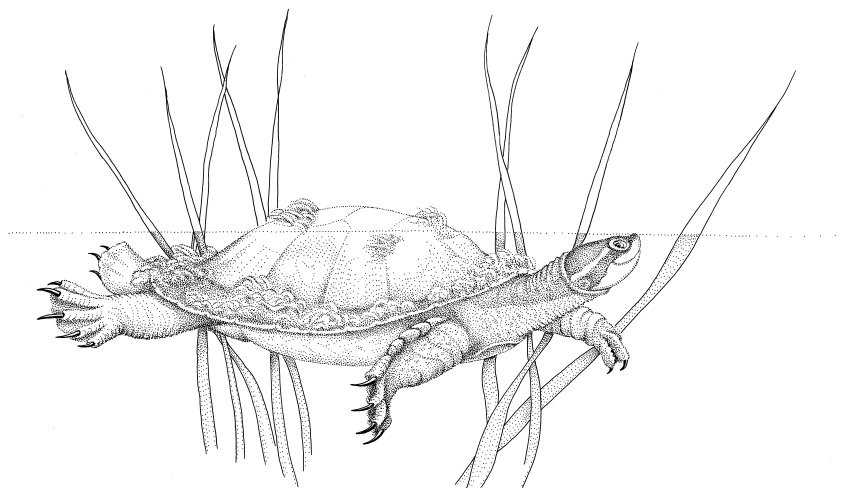


Figure 17.5 Aquatic basking posture of the chelid, *Emydura krefftii*. (After photo by J. Cann/ANT) [T. Wright]

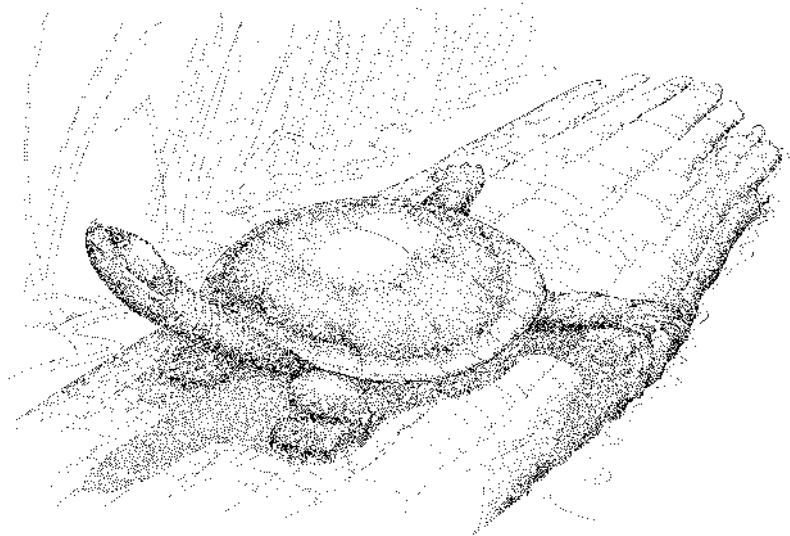


Figure 17.6 Aerial basking posture in the chelid, *Emydura macquarii*.
[T. Wright]

Pseudemys (Moll & Legler 1971). These consist of tear secretion, gular movements, panting, frothing from the mouth and wiping tears or water over the surface of the head. *Chelodina expansa* and *C. longicollis* bask only occasionally (Webb 1978).

Of the marine turtles, only *Chelonia mydas* leaves the water to bask and does so most frequently at breeding time (Whittow & Balazs 1982; Garnett & Crowley 1985). *Chelonia mydas*, *Caretta caretta*, *L. olicacea* and *N. depressus* may bask by floating high at the water surface (Sapsford & van der Reit 1979; Limpus unpub. data). During sunny days basking can result in elevated body temperatures (Whittow & Balazs 1982; Sapsford & van der Reit 1979). However, since *C. mydas* will bask on beaches even at night when they would be losing heat, it is doubtful if these basking activities are always primarily for thermoregulation (Garnett & Crowley 1985; Limpus unpub. data).

ECONOMIC SIGNIFICANCE AND MANAGEMENT

Research

Research on freshwater turtles for management purposes requires information on distribution and abundance, in order to assess the current population status of the species, to determine its specialisation for particular microhabitats, and to establish a baseline for monitoring population trends. Hoop traps, baited with bread, sardines, meat, fish or a combination of these, are most useful for capturing freshwater turtles (Legler 1960a). Hoop traps yield samples of *Emydura krefftii* (Fraser Island) that are unbiased with respect to size and sex (Georges 1985).

Capture rates of turtles in baited hoop traps in the Northern Territory are very low, with notable exceptions, and a modification of the design to enable accumulation of turtles over a period of days or weeks has been developed by Kennett (1992). Diving may be precluded by risk of attack by saltwater crocodiles. Turtles can be collected in relatively clear waters using a dip-net and spotlight from a punt at night. This is particularly successful for capturing *Carettochelys insculpta*, *Emydura victoriae* and *Elseya dentata*. Baited traps readily catch *Chelodina longicollis*, *C. rugosa* and all species of *Emydura* and

Elseya, but they are of limited use with *C. expansa* and *Pseudemydura umbrina*, species which feed principally or solely on live animals. Other methods of capture are discussed in Chapter 14.

Chelid turtles can be permanently marked by cutting notches in the marginal scutes and underlying peripheral bones with a file or small hacksaw. A semi-binary code is preferable to minimise the number of adjacent notches in any one quarter of the carapace. Notching is inappropriate for *Carettochelys insculpta*, which lacks scutes. Further, the carapace margin is well-vascularised, and cutting the peripheral plates, visible beneath the overlying skin, results in unacceptable bleeding and such notches are not permanent (Georges & Kennett 1988). Though cattle ear tags can be attached to the shell through a hole drilled in the lateral margins of the carapace, these are only useful for one to two years. A tagging system similar to that used on marine turtles (Limpus 1992b), or freeze branding, are alternatives worthy of investigation for marking this species.

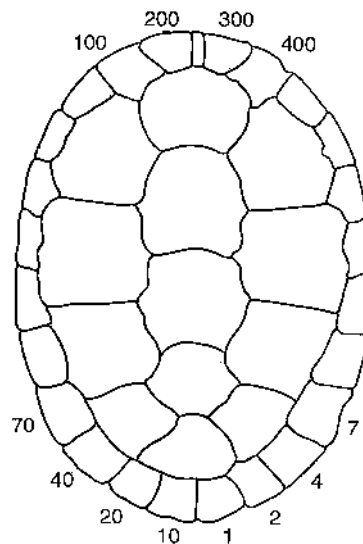


Figure 17.7 Diagram showing the marking scheme used to identify individuals of *Emydura krefftii*. Notches are cut into the marginal scutes and underlying peripheral bone with a file or small saw, to form a permanent and unique pattern. Individuals are identified by adding the numbers assigned to particular scutes; for example turtle number 3 is marked by notching scutes 1 and 2 on the right rear of the carapace. [D. Wahl]

Once a marked population is established, it is possible to estimate population sizes using one of many mark-recapture techniques (Seber 1973). Catchability among individuals varies considerably (Georges 1982a) and use of techniques catering for such variation, such as the regression methods or frequency of capture methods (Seber 1973), should be explored as alternatives to the traditional Peterson and Jolly-Seber methods, unless sampling intensity is high (>75% of the population marked).

Traditionally, reproductive biology of freshwater turtles has been studied by killing turtles on a monthly sampling basis and examining the reproductive organs (Georges 1983). However, such destructive sampling is rapidly becoming ethically unacceptable, and is not feasible for assessment of species at risk. Radiography (Gibbons & Greene 1979), laparoscopy (Limpus & Reed 1985a) and ultrasound scanning (Kuchling 1989) provide practical alternatives to dissection and direct examination of reproductive organs. Radiography can

detect and allow counting of shelled oviductal eggs, but soft parts such as corpora lutea or enlarged ovarian follicles are not revealed. Long-term effects of repeated exposure of turtles to X-rays is not known.

Gonadal structure can be examined, measured and biopsied by laparoscopy, but there are limitations on accurate counting and some measurements (Limpus 1992a). Ultrasound scanning is an accurate method to measure and count large structures such as eggs and follicles. However, there are limitations on the depth of reliable viewing with large animals, and small structures, such as corpora albicantia, may not be resolved in the images produced. Though these new technologies have their strengths and weaknesses, they have the potential to contribute significantly to population studies.

Stomach contents can be obtained by stomach flushing (Legler 1977). A 12V submersible pump is used to supply a steady flow of water, which is passed into the stomach through a flexible plastic tube (Georges *et al.* 1986). The water then passes back up the oesophagus carrying food particles with it. Water flow is adjusted for turtles of different sizes by interchanging tubes of different diameters. The food particles are caught in gauze and transferred to 70% ethanol for later sorting and identification.

Percentage composition of the diet by number, weight or volume, and occurrence (Windel & Bowen 1978) are traditionally used to assess the relative importance of various food types in the diet. Caution must be exercised in the interpretation of diet from stomach contents, as the proportional representation of foods in the stomach does not reflect diet in a strictly quantitative sense. Different foods differ in their digestibility and rate of passage through the gut. Nor do animals forage at random, so foods found in the stomach of an individual at one time do not necessarily provide a random selection of foods eaten by that individual over time. To assess the degree of dietary specialisation, one must compare the foods eaten with the foods potentially available in the environment, either qualitatively or quantitatively (Georges *et al.* 1986).

Criteria for Setting Conservation Priorities

Australian freshwater turtles do not often fall into the category of species in conflict with community goals, values and aspirations. Nor are they a major economic resource, at least for Australian communities. Priorities for their conservation must therefore be based on values that cannot be measured on an economic scale.

There are three intrinsic attributes with a bearing on the conservation priority accorded a species. The first is distinctiveness, important because it may enhance both its aesthetic and scientific value. If a species is taxonomically distinct, then it will lack close relatives which may share some or many of its features, and much may be lost if such a species becomes extinct. The second attribute is rarity. Rarity in the colloquial sense may increase the aesthetic value of a species, and so increase public pressure for adequate conservation measures. Rarity in the biological sense combines both abundances and distribution (Rabinowitz, Cairns & Dillon 1986). An abundant species with a geographically restricted distribution can be quite vulnerable to extinction through habitat destruction, climatic change or disease, whereas an ubiquitous species with low abundances throughout its range may be quite secure. The third attribute is a species' intrinsic vulnerability to decline and eventual extinction. Rarity, low fecundity, susceptibility to disease, specialisation on particular foods or other environmental attributes are all examples of factors contributing to a species' vulnerability to extinction.

Extrinsic factors also have a role to play in setting conservation priorities. Are there current threats to populations, and is there a pressing need for intervention to negate or offset the deleterious effects of human activities or natural events?

Opposing factors include logistic constraints—whether they be legal, economic, social or biological—that diminish the feasibility of conservation measures or render them impractical. Feasibility must be gauged against the objectives of management, namely to preserve the current Australian turtle diversity by preventing further extinctions. A second objective, and one that requires more investment to achieve, is to conserve species in the context in which they evolved so that we also preserve the processes that maintain genetic diversity and lead ultimately to speciation.

Conservation Priorities

Among freshwater forms, *Pseudemydura umbrina* sits high on the list of priorities. It is distinctive both taxonomically and morphologically. It represents a monotypic genus, and its nearest living relatives may be among the chelids of South America (Legler 1981). The species is exceptionally rare (Burbidge 1981; Kuchling & DeJose 1989), being restricted to a wild population of less than 30 individuals near Perth in Western Australia. It is vulnerable by its inflexible preference for ephemeral waters, even when permanent water is available and accessible (Burbidge 1983), in a climatic regime where its habitat is flooded in the colder months of the year. It also has the lowest fecundity of any Australian chelid, laying only one clutch of three to five eggs per season. The species is threatened by habitat loss through past draining of swamps for land reclamation and by predation on eggs and adults by introduced foxes, which are devastating predators of freshwater turtles throughout their range (Parmenter 1976; Thompson 1983; Palmer-Allen *et al.* 1991). Current measures are directed at captive breeding and re-introduction to an area within its former range (Burbidge, Kuchling, Fuller, Graham & Miller 1990; Kuchling & Bradshaw 1992; Kuchling & DeJose 1989; Kuchling, DeJose, Burbidge & Bradshaw 1992).

Carettochelys insculpta is Australia's most distinctive turtle, both morphologically and taxonomically. It is the sole remaining species in its family, and as such represents all that remains of 40 million years of evolution independent of any other extant lineage (Chen, Mao & Ling 1980). The species was once considered to be one of the rarest turtles in the world (Groombridge 1982), but it now appears that where it is found, it may be locally quite abundant (Georges & Kennett 1989). It is rare in the sense of being geographically restricted, as a family, to southern New Guinea and northern Australia. In Australia, it is distributed from the Victoria River in the west to the Goomadeer River in the east, but abundant only in the Daly and Alligator drainages. The species is vulnerable by virtue of its limited distribution, and because stereotyped nesting habits render it susceptible to over-exploitation. Adults and their eggs are highly regarded as food by indigenous peoples throughout its range, and exploitation for food is thought to be threatening populations in New Guinea (Groombridge 1982). Habitat degradation is the major potential threat to Australian populations (Georges 1988b).

Third on our list of priorities for freshwater turtles is *Rheodytes leukops*. It is distinctive enough to be placed in a monotypic genus, and has no clear affinities with any other Australian freshwater turtle (Georges & Adams 1992). Morphologically, it is quite striking because of its capacity to extract oxygen from water using well-vascularised gills in a well-ventilated cloaca (Chapter 16). The species is restricted to a single drainage, the Fitzroy-Dawson system of central Queensland, and while there are no data on abundances, it is considered quite rare by virtue of its limited distribution. The species is vulnerable as a result, and because it is specialised for life in the riffle—fast flowing broken water. With increasing numbers of dams and weirs, riffle is an endangered microhabitat. The biology of *Rheodytes leukops* is poorly known, and its conservation priority may change with further study.

Other distinctive species are largely ignored during considerations on conservation, because they are so poorly studied. Many are undescribed. The three undescribed species of *Elseya* in New South Wales, the new genus colloquially known as shortnecked alpha, the Arnhem Land *Chelodina* are all restricted in distribution, but nothing is known of their biology or population status. *Emydura subglobosa* of the Jardine River on Cape York, is rare, but not considered a high priority because it is not taxonomically distinct above the species level and it is common in New Guinea.

Rare species are not the only ones to attract the attention of conservation biologists. Recent biochemical studies (see Georges & Adams 1992) have shown *E. macquarii* from the Murray-Darling drainage, *E. krefftii* from coastal Queensland and *E. signata* from coastal New South Wales to be a single species, sharing even rare alleles. However, morphological and genetic variation suggest that they are in the process of allopatric speciation. This speciation process could be brought to an abrupt halt if exchange of specimens between drainages is artificially enhanced, say by distribution of hatchling *Emydura* by the pet trade. In contrast, specimens of *Chelodina longicollis* frequently migrate overland and may easily migrate from drainage to drainage. Genetic and morphological variation throughout its range is slight, and commercial distribution of hatchlings and subadults would have little impact on genetic processes leading to speciation. These are important considerations if we are to address seriously the second conservation objective listed above.

Among the marine turtles, *C. caretta* populations that nest in eastern Australia, have declined by more than 50% in the past decade. This decline has been attributed mostly to accidental drowning in fishing gear in Australian waters (Limpus & Reimer in press). There is wide spread and large-scale hunting of *C. mydas* and *E. imbricata* populations that nest in northern Australia. There is no evidence to suggest that the populations are large enough to support the current harvests in the long term. The small number of *L. olivacea* which drown in fishing gear annually in Australia may be excessive for the small nesting populations that occur in Australia. For these species at least, there must be concern for the long term viability of the species in Australia and active conservation management of their populations is required both in Australia and in neighbouring countries.

Management must address a wide range of problems which may be grouped into three broad areas: fishing, development and predation by feral animals. Traditional and commercial harvests of turtles are often carried out in remote areas where enforcement is difficult; fishermen are often reluctant to modify fishing gear in order to reduce turtle capture and death. Development of coastal areas for tourism, agriculture and real estate have negative impacts on turtle nesting and feeding habitat. Predation of eggs and hatchlings by feral foxes and pigs in Queensland may result in future declines in *C. caretta* and *N. depressus* populations.