

Vertebrates of desert rivers: meeting the challenges of temporal and spatial unpredictability

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INTRODUCTION

Vertebrates, the 'charismatic megafauna' of desert rivers, form a minute part of the biodiversity dependent on flows. Despite their numerical insignificance, they are particularly important to humans for food (e.g. fishes) or conservation (e.g. mammals and waterbirds); given our impact on the ecology of these unique systems, this makes them an essential component of the ecology of desert rivers. They also play an important functional role as top-level predators, affecting prey abundance, or sometimes shaping habitat availability and extent (e.g. by enlarging waterholes). Vertebrates are often the focus for conservation effort and policies, with declines in waterbird and fish populations forcing changes, albeit belated, to river management (Lemly *et al.*, 2000; see Chapter 8, this volume).

There are thousands of species over all the major groups of vertebrates (fishes, amphibians, reptiles, birds, mammals) dependent on desert rivers of the world. Aquatic vertebrates are obviously directly dependent on desert rivers but other more 'terrestrial' vertebrates, including elephants, birds of prey (e.g. fish eagles) and small mammals

(Briggs, 1992), have life histories significantly affected by flooding and drying patterns of rivers. This chapter focusses primarily on aquatic vertebrates but also includes more terrestrial species dependent on riparian areas and water from rivers. Treatment of these more terrestrial groups is not exhaustive. The presence and availability of water for these species is essential for survival, particularly as a source for drinking and refuge from, or area for, predation. Survival and reproduction of many vertebrate species depend on the spatial and temporal disturbance patterns of desert rivers. From its source, the desert river forms habitats that range from riparian corridors along the river to the terminal lakes, estuaries and floodplains, sometimes extending more than 1000 km. In the lower parts of the river, the aquatic habitats provide complex food webs for vertebrates in an otherwise poorly resourced desert landscape. It is no accident that biodiversity around wetlands in the desert is spectacularly high (e.g. Lake Manyara, Tanzania; Okavango Swamp, Botswana; Macquarie Marshes, Australia).

One vertebrate species now dominates the ecology of most desert rivers. Our role is pervasive, often irrevocably changing a river's ecology and disturbance regimes with river regulation (see Chapters 8 and 11, this volume). Besides water resource development, fishing is probably the most important ecosystem service for people living on desert rivers (Thomas, 1995). In addition, vertebrates now underpin the economies of wildlife tourism in many desert regions of the world (e.g. Okavango) (Ellery & McCarthy, 1994). There is also a tradition for hunting waterfowl for sport, emanating from the northern hemisphere (Kear, 1990), which contributes to local economies. Albeit not at the same scale, other exotic species of vertebrate, particularly fishes, have also significantly changed the ecology of desert rivers.

Despite the human focus on vertebrates, our understanding of their ecology and interaction with desert rivers and disturbance regimes remains relatively superficial (Nilsson & Dynesius, 1994), even for fish ecology. This is also attributable to the lack of research effort on vertebrates in desert regions (Kingsford, 1995) until relatively recently. The combination of spatial and temporal variability of desert rivers and extensive movement patterns of vertebrates, laterally and longitudinally, has also probably hampered our understanding. In this chapter we review current knowledge of vertebrate groups and their interactions with disturbance flow regimes in desert rivers. Rather than adopting an evolutionary classification order, we present the groups from most aquatic to least aquatic (fishes, amphibians, birds, reptiles and mammals).

HABITATS

Most large desert rivers begin in higher-altitude and more mesic regions of the world before they flow across desert regions (< 500 mm rainfall per year; e.g. Nile, Colorado, Murray–Darling, Tigris–Euphrates, Tarim) (see Chapter 1, this volume). These rivers are often sediment-laden and often flood large broad floodplains, wetlands or estuaries with relatively low gradient (see Fig. 7.1). Some desert rivers originate in areas of higher elevation, with high gradients and variable rainfall producing unpredictable brief flash floods. A lateral dimension matches the longitudinal one, producing different habitats: channels, waterholes, riparian corridors, floodplains, swamps, lakes, springs, depressions and estuaries (Fig. 7.1; Table 7.1). These categories provide a reference point for a discussion of different dependencies of vertebrates in three main regions: the upper, mid and lowland parts of a desert river. Although no river can be divorced from its catchment, we confine our discussion to where rivers flow or flood temporarily or permanently across deserts.

Large desert rivers can begin as small permanent streams in a mesic upper catchment, providing habitat for amphibians and a source of water for terrestrial vertebrates. Networks of tributary creeks and streams in the upper catchments of all desert rivers funnel flow into the main stem of a river system. Distinctive riparian vegetation usually grows along the tributary creeks and the main river in the upper catchment, providing an important ecotone between terrestrial and aquatic systems (Table 7.1) (Malanson, 1993). In the upper catchment, vegetation diversity, distribution and structure usually reflects high rainfall and the aquatic parts of the river are primarily confined to the channels or narrow floodplains. These provide habitat for fish species (tolerant of low temperatures), some turtles and a few specialist mammals. Most vertebrates using this part of the river are terrestrial species, drinking, bathing or preying on other animals (Table 7.1). Exotic fish species (e.g. trout species) may thrive in low temperatures exacerbated by hypolimnetic releases from storages (King *et al.*, 1998). Large storages in the upper catchment of a desert river are usually deep and provide poor habitat for many vertebrate species, such as waterbirds or riverine native fishes (Minckley, 1973).

For most aquatic vertebrates (fish may be an exception) the river in the upper part of the catchment plays more of a functional role, transporting nutrients and organic matter from nutrient-rich and

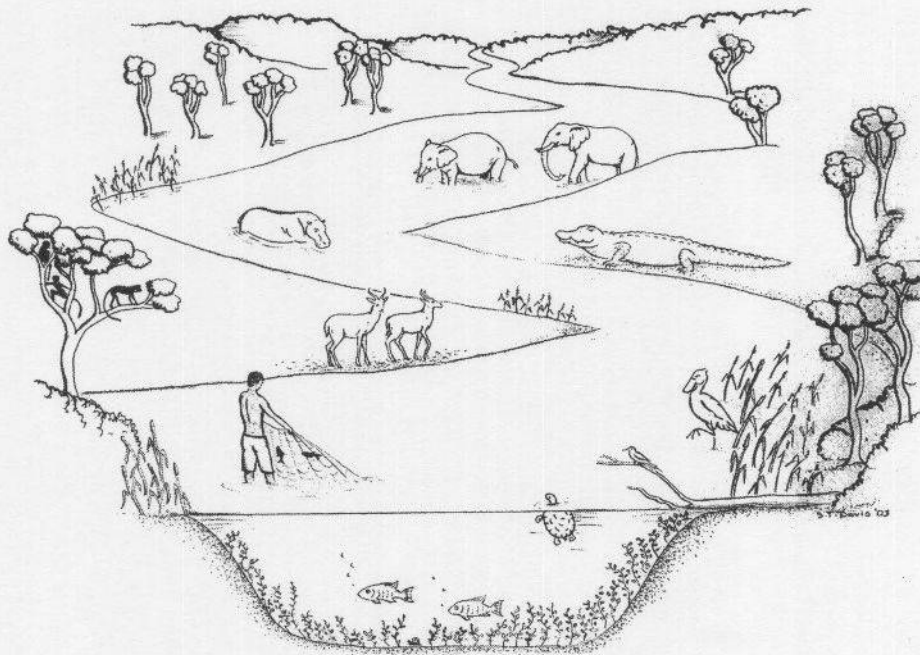


Figure 7.1. Schematic of vertebrates using a hypothetical African desert river system that starts in mountain ranges and ends in a large terminal wetland.

biodiverse vegetation communities to the mid and lower parts of the river. Most of the available aquatic habitats for vertebrates, in terms of diversity and extent, lie in the lower parts of desert rivers (Fig. 7.1). Waterholes and channels in the lower parts of a desert river (Table 7.1) often provide permanent habitat (Knighton & Nanson, 1994) for totally aquatic species (e.g. turtles, crocodiles (Fig. 7.2), fishes) when evaporation dries floodplain and wetland habitats. Floodplains are the most extensive areas on desert rivers (Kingsford *et al.*, 2001). Although floodplains are usually inundated for less than a year, complex vegetation diversity and abundance allow many terrestrial and aquatic vertebrates to survive and reproduce.

Large deltas often occur in the lowland regions of a desert river and these form relatively permanent wetland systems dependent on flows from desert rivers (Table 7.1). They are most extensive in the terminal parts of large desert rivers (Lemly *et al.*, 2000). Deltas are made up of complex permanent, semi-permanent and temporary aquatic habitats, with different inundation and drying frequencies. These habitats usually include extensive swamps, reed beds and lagoons as well as

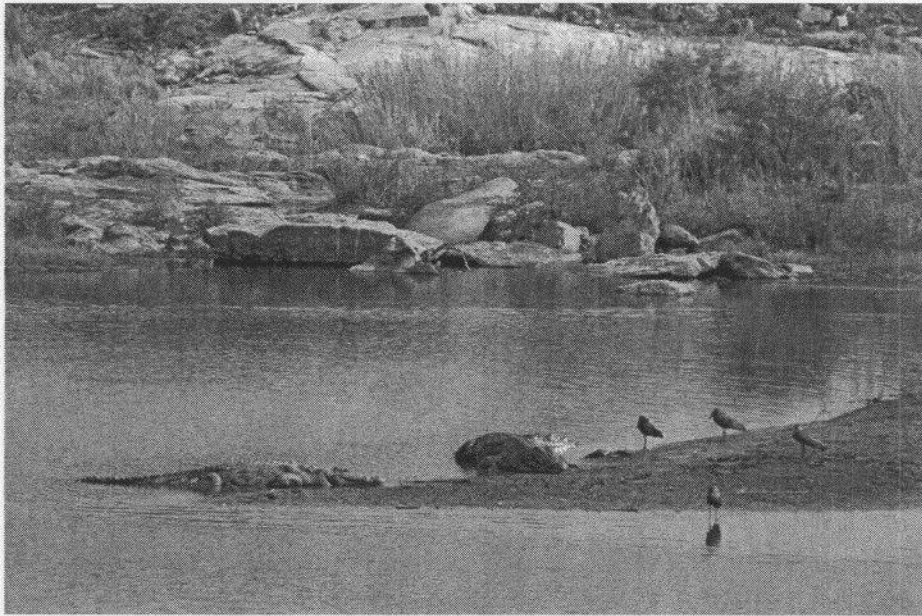


Figure 7.2. Nile crocodiles *Crocodylus niloticus* in the Sabie River, a semi-arid river in South Africa, prey on fishes and herbivores when they come to drink. Birds such as these hammerkops *Scopus umbretta* feed on frogs, fishes and aquatic invertebrates that live in desert rivers (Photo K. Rogers).

distinct river channels and woodland floodplains. This results in a complex array of different habitats for terrestrial and aquatic vertebrates (Table 7.1; Fig. 7.1). Freshwater and saline lakes form another distinctive feature of desert rivers (Table 7.1). Generally, salt lakes are connected to more temporary and smaller desert rivers or local catchments (Kingsford *et al.*, 2001), although some terminal basins of large rivers also become saline as they dry (e.g. Lake Eyre, Australia). Salinity in saline lakes varies with patterns of freshwater inflows. Some large freshwater lakes in desert regions often retain water for long periods, sometimes almost permanently (Timms, 1998, 2001). The remaining aquatic habitats are classified as claypans or depressions (Timms & Boulton, 2001) (Table 7.1). These predominantly obtain water from small creeks or local runoff. All these diverse habitats provide essential and sometimes distinctive habitat for a broad suite of vertebrate species.

FISHES

There are more than 10 000 freshwater fish species (Matthews, 1998), many more than any other group of vertebrates. Fishes are abundant in

Table 7.1. Different habitats and their use by vertebrates dependent on desert rivers (see Fig. 7.1) in the upper, middle and lower parts of a desert river catchment

Location in the river: upper (U), middle (M) and lower (L).

Habitat	Location	Description and use by vertebrates	Vertebrates
Storage or dam	U	Relatively little shallow water but may allow growth of small amounts of aquatic vegetation, forming habitat for aquatic vertebrates	Fish species typical of lentic conditions. Terrestrial vertebrates drink and bathe. Some waterbirds (e.g. piscivores) but generally poor habitat
Spring	U, M, L	Usually relatively small areas with distinctive ecological communities, including fish and amphibian communities. Terrestrial vertebrates drink and bathe in springs	Unique habitat for fish species and some frogs. Used by few other aquatic vertebrates but some terrestrial vertebrates (e.g. passerine birds)
Channel	U, M, L	Usually relative narrow band of flowing water in upper catchment. Used for drinking and bathing by most vertebrates, apart from fish and turtle species. Increasing volume and width of water in mid and lower catchment, structurally more complex with different instream habitats (e.g. benches, wood)	Fish species, forest-dwelling mammals (e.g. monkeys, antelope), snakes (tree snakes) and birds (parrots) and some specialist mammal species (e.g. platypus, otters). In mid to lower parts, fish number and diversity high, increasing numbers of turtles and mammals (e.g. water rats, elephants, waterbuck). Focus for fish-eating birds (e.g. pelicans, cormorants)

Table 7.1. (cont.)

Habitat	Location	Description and use by vertebrates	Vertebrates
Riparian corridor	U, M, L	Habitat formed between the main river channel and terrestrial areas for aquatic and terrestrial vertebrates. Vegetation attracts herbivorous or fruit-eating vertebrates. In mid to lower sections, area increases	Birds and mammals feeding on fruits, seeds and vegetation (e.g. fruit pigeons, bats). Increasing diversity and abundance of terrestrial species using the structural and diverse vegetation (e.g. honeyeaters, bee-eaters, koalas, tree frogs, elephants, monkeys)
Waterholes, billabongs, wadis	M, L	Deep parts of the channel that produce refuge areas during dry periods for aquatic fauna, as these areas seldom dry out	Fish and turtle abundance high. Provide nesting habitats for waterbird species, particularly piscivores.
Floodplain	M, L	Usually increases with longitudinal distance down the catchment. Frequency of inundation determines vegetation composition. During floods extensive habitat created for aquatic and some terrestrial vertebrates, particularly for breeding	High diversity and abundance of fishes, frogs, waterbirds, aquatic reptiles and mammals in feeding and breeding areas. Terrestrial vertebrates also breed (e.g. budgerigars, raptors) during floods. Dry floodplains provide habitat for terrestrial vertebrates: birds, small and large mammals and reptiles
Swamps	M, L	Generally perennial areas with complex aquatic vegetation. Provide habitat, feeding and breeding, for all major aquatic groups, with considerable use by terrestrial vertebrate species	Probably area of desert rivers with highest abundance and diversity of all groups of aquatic and terrestrial species (e.g. African buffalo, cranes)

Lake	M, L	Freshwater and salt lakes that usually hold water for longer than floodplains and provide extensive feeding habitats for aquatic species, particularly waterbirds and fishes. Terrestrial species converge on lakes for drinking and bathing	Usually high biodiversity and abundance of waterbirds and fishes. Specialised habitat for some fish species (e.g. lungfish). Salt lakes may have specialised vertebrates (e.g. flamingos) as well as other waterbirds. Terrestrial species (e.g. waterbuck) often found around margins
Depression or claypan	M, L	Relatively small freshwater wetlands inundated by local rainfall; usually highly turbid. Provide habitat for frogs and waterbirds in particular, and drinking habitat for terrestrial vertebrates	Feeding and breeding habitat for frog species and feeding habitat for waterbirds
Estuary	L	The terminal part of desert rivers flowing out to sea. Highly productive ecosystem created between freshwater and marine processes	Includes many fish species of marine and freshwater origin. Waterbirds, particularly fish-eating and migratory wading birds, collect in large numbers on some estuaries of dryland rivers

desert regions (Table 7.1), despite most people's impressions. Desert rivers and local rainfall create extensive aquatic habitat with diverse and productive food webs for fishes (Bunn *et al.*, 2003; Chapters 4, 5 and 6, this volume). But it is the temporal and spatial dynamics of this habitat that strongly influence desert fish populations: the droughts and floods. Not surprisingly, our current knowledge of fish ecology from desert regions of the world is relatively poor, with most published studies coming from North America (Deacon & Minckley, 1974; Minckley & Deacon, 1991) and Australia (Merrick & Schmida, 1984; Wager & Unmack, 2000; Arthington *et al.*, 2005). Information on fishes from other desert regions is largely limited to taxonomic and distributional accounts (Table 7.2): Middle East (Bannister & Clarke, 1977; Al Kahem & Behnke, 1983; Krupp, 1983, 1988; Ross, 1985; Krupp & Schneider, 1989; Krupp *et al.*, 1990; Coad, 1991; Victor & Al-Mahrouqi, 1996; Goren & Ortal, 1999); Eurasia (Afghanistan (Coad, 1981)); and Africa (Beadle, 1974; Roberts, 1975; Dumont, 1982; Skelton, 1986; Lévêque, 1990).

Many extant fish species in deserts reflect effects of past climates and geomorphology because fish movement between isolated catchments is restricted (Minckley *et al.*, 1986; Unmack, 2001b). Progressive aridity has filtered fish species occurrence, as habitats recede and change from glacial periods (every 100 000–150 000 years) to long-term climate changes (more than one million years). For example, there are dozens of isolated basins throughout the Great Basin of North America with and without fish fauna (Hubbs & Miller, 1948; Hubbs *et al.*, 1974; Smith *et al.*, 2002). Ten thousand years ago, many of these basins contained large lakes filled from melting glaciers that spilled into successive basins. With increasing aridity, large lakes and streams disappeared, leaving a few small springs as fish habitat. Fish species unable to persist in these small springs disappeared. Similar processes shaped desert fish faunas in all deserts, including those of Australia (Wager & Unmack, 2000), Africa (Dumont, 1982; Lévêque, 1990) and the Middle East (Mirza, 1986; Krupp, 1983, 1987; Coad, 1987; Por, 1989).

The distribution of water and spatial and temporal variability of flooding and drying patterns dominate the ecology of fishes living in desert rivers, producing life-history traits that allow them to survive droughts and major floods while capitalising on the benefits derived from floods. Local geomorphology determines water permanence, which determines fish occurrence (Unmack, 2001a; Arthington *et al.*, 2005). In some desert rivers of Australia, fine clay sediments seal the

Compiled from Orange River, Africa (OR) (Skelton, 1986); Sahara Desert (SD), Africa (Dumont, 1982; Lévêque, 1990); Arabian Peninsula (AP) (Al Kahem & Behnke, 1983; Krupp, 1983); Jordan River/Israel (JR) (Krupp & Schneider, 1989; Goren & Ortal, 1999); Iran (I) (Coad, 1987); Tigris–Euphrates rivers (Coad, 1991); Afghanistan (AF) (Coad, 1981); Central Asia (CA) (Petr, 1999); North America (NA) (DFC, 2003); and Australia (AU) (Unmack, 2001b). Note that some fishes occur in the Namibian Desert but species were not recorded (Day, 1990) and that no information was available for South America. Species numbers for Central Asia probably substantially underestimate the number of fish species.

[illegible]

Table 7.2. (cont.)

Common names	Taxonomic group	No.	OR	SD	AP	JR	I	TE	AF	CA	NA	AU
Schilbid catfishes	Schilbeidae	4	-	-	-	-	-	-	1	3	-	-
Sheathfishes	Siluridae	16	-	-	-	-	2	2	5	7	-	-
Sisorid catfishes	Sisoridae	50	-	-	-	-	4	5	7	34	-	-
Clingfishes and singleslits	Gobiesocidae	1	-	-	-	-	-	-	-	-	1	-
New World silversides	Atherinopsidae	2	-	-	-	-	-	-	-	-	2	-
Old World silversides	Atherinidae	8	-	-	-	-	1	-	-	-	-	7
Rainbowfishes	Melanotaeniidae	3	-	-	-	-	-	-	-	-	-	3
Pupfishes	Cyprinodontidae	47	-	4	2	3	4	5	-	3	33	-
Topminnows and killifishes	Fundulidae	5	-	-	-	-	-	-	-	-	5	-
Poeciliids	Poeciliidae	32	-	-	-	-	-	-	-	-	32	-
Splitfins	Goodeidae	14	-	-	-	-	-	-	-	-	14	-
Sticklebacks	Gasterosteidae	2	-	-	-	-	1	-	1	-	1	-
Pipefishes and seahorses	Syngnathidae	1	-	-	-	-	1	-	-	-	-	-
Mulletts	Mugilidae	5	-	-	-	2	1	1	-	-	3	-
Asiatic glassfishes	Ambassidae	2	-	-	-	-	-	-	-	-	-	2
Temperate basses	Percichthyidae	3	-	-	-	-	-	-	-	-	-	3
Sunfishes	Centrarchidae	5	-	-	-	-	-	-	-	-	5	-
Grunters and tigerperches	Terapontidae	6	-	-	-	-	-	-	-	-	-	6
Drums and croakers	Sciaenidae	1	-	-	-	-	-	-	-	-	1	-
Perches	Percidae	16	-	-	-	-	3	-	3	4	8	-
Cichlids	Cichlidae	22	2	5	-	7	1	-	-	-	8	-
Sleepers and gudgeons	Eleotridae	18	-	-	-	-	-	-	-	-	5	13
Gobies	Gobiidae	33	-	-	-	-	24	3	1	-	2	3
Combtooth blennies	Blenniidae	1	-	-	-	1	-	-	-	-	-	-
Sculpins	Cottidae	6	-	-	-	-	-	-	-	1	5	-
Spiny eels	Mastacembelidae	3	-	-	-	-	1	1	1	1	-	-
Totals		1076	14	29	16	33	151	68	121	346	269	46



Figure 7.3. This endangered desert fish, the humpback chub *Gila cypha*, lives in canyon-bound reaches of the Colorado River, where it depends on variable river flows (Photo P. J. Unmack).

bottom of waterbodies, preventing water loss by infiltration and creating permanent or semi-permanent aquatic habitats (Knighton & Nanson, 2000). In deserts with high stream gradients, deep alluvial sedimentary basins act as sinks that fill with water; when these are intersected by impervious geological strata (e.g. canyon walls), water is forced to the surface, providing permanent and flowing reaches of streams. This provides distinctive permanent habitat for desert fish species in parts of North America (e.g. Colorado River Basin) (Fig. 7.3), the Middle East and parts of central Australia (e.g. The MacDonnell Ranges) (Minckley, 1991; Unmack, 2001a).

Most desert fish species are habitat generalists with a broad diet. They opportunistically capitalise on times of plenty after flooding but also withstand dry times when there is less food. Desert fishes have no unique adaptations compared with other fishes (see Deacon & Minckley, 1974), but they have broad tolerances to high temperature, high suspended solids, low oxygen concentrations and high salinity (Beumer, 1979; Gehrke & Fielder, 1988; Deacon & Minckley, 1974; Wager & Unmack, 2000). Several desert fishes have small and deeply embedded scales that may reduce abrasion due to turbidity (e.g. most native minnows

in the Colorado River Basin (Fig. 7.3), golden perch *Macquaria ambigua* from Australia). The woundfin *Plagopterus argentissimus* (Colorado River Basin) has specialised barbels around the mouth for feeding in turbid conditions (Minckley, 1973). A few species are long-lived (25–45 years) (Minckley & Deacon, 1991; Mallen-Cooper & Stuart, 2003), allowing them to survive many years without recruitment. These include several North American catostomid (e.g. razorback sucker *Xyrauchen texanus*, cui-ui *Chasmistes cujus*) and cyprinid fishes (e.g. Colorado pikeminnow *Ptychocheilus lucius*, humpback chub *Gila cypha* (Fig. 7.3)) and several Australian percichthyids (e.g. Murray cod *Maccullochella peelii*, golden perch). All long-lived species usually have high fecundity with several hundreds of thousands to a few million eggs (Minckley & Deacon, 1991; Merrick & Schmida, 1984).

Fishes living in deserts need to survive dry periods when floods recede. No true desert fishes survive without water as adults or eggs (aestivation), except African lungfishes *Protopterus* spp. from mesic and semi-arid regions, with biseasonal patterns of wet and dry seasons. They survive low oxygen concentrations and drying, buried in the mud, as they can breathe air. Eggs of some killifishes (Cyprinodontiformes) from Africa and South America, living in dry tropical seasonal areas, have to dry out each year before they can hatch (Helfman *et al.*, 1997). Other desert fishes survive short dry periods. The longfin dace *Agosia chrysogaster* (Colorado River Basin) survived for 14 days after evapotranspiration removed surface water until rainfall replenished the creek. They sheltered under algal mats during the day and fed at night when water was present (Minckley & Barbour, 1971). Similarly, spangled perch *Leiopotherapon unicolor* and catfish (Plotosidae) were alive in drying mud at the bottom of waterholes in Australia (Wager & Unmack, 2000). In Australia, desert fishes concentrate in permanent waterholes most of the time, with little available food, few opportunities for reproduction, declining oxygen concentrations, increasing salinity and high levels of predation. Here, there is little or no baseflow, sometimes lasting months or perhaps years (Walker *et al.*, 1995; Puckridge *et al.*, 2000). Eventually desert rivers dry up, trapping fishes with rising salinity causing massive mortality (Ruella, 1976; Kingsford & Porter, 1993; Arthington *et al.*, 2005).

Flooding is essential for desert rivers, often producing complex habitats for fishes in three ways, varying with stream channel type and sediment load. First, massive floods fill deep parts of a river while small floods scour the river bottom, removing sediment and forming large deep pools or waterholes (Deacon & Minckley, 1974; Graf, 1988;

Unmack, 2001a). Second, floods inundate floodplains and fill semi-permanent wetlands (Puckridge *et al.*, 2000; Sheldon *et al.*, 2002). For example, during major floods Cooper Creek in Australia changes from a string of isolated waterholes to a vast inundated floodplain (Puckridge *et al.*, 2000; Roshier *et al.* 2001a; Arthington *et al.*, 2005). Lastly, floods fill local groundwater basins that maintain surface water through major droughts by seepage (Minckley, 1991). Fish breeding is often related to flooding or rises in water levels, reflecting the temporal and spatial variability of flow regimes in desert rivers. Not all desert rivers are the same, with some having deeply incised channels and infrequently flooded floodplains. Many desert fishes reproduce or migrate in response to flooding, but only a few species require flooding or a rise in water level to stimulate reproduction. These include Welch's grunter *Bidyanus welchi*, silver perch *B. bidyanus* and golden perch from Australia (Merrick & Schmida, 1984). In dry years some species still have limited reproduction (Humphries *et al.*, 1999; Wager & Unmack, 2000) but massive breeding only occurs during years with large floods (Puckridge *et al.*, 2000; Wager & Unmack, 2000; Hocutt & Johnson, 2001). Within the Colorado River Basin, spawning for most species extends over many months because there is little variability in flow without rainfall (Minckley, 1973). However, higher rainfall years typically produce more native fishes (P. Marsh, personal communication). Some North American species (e.g. speckled dace *Rhinichthys osculus*) spawn immediately after a flood rearranges the substrate (Deacon & Minckley, 1974). In the Orange River in South Africa, most fish species spawn during spring and summer in response to higher flows (Skelton, 1986). In the variable flows of Cooper Creek in Australia, there was high variability among years in reproduction and recruitment of fishes (Puckridge *et al.*, 2000). In floodplain areas with large quantities of organic matter or toxic chemicals from plants (e.g. *Eucalyptus* spp.), floods are not always immediately beneficial to fish populations as they leach out tannins from vegetation, causing mortality (Gehrke, 1991; Gehrke *et al.*, 1993). In addition, small freshwater inflows may increase nutrient concentrations and stimulate algal growth that may deplete oxygen levels and result in mortality and lesions in native fish populations (e.g. Diamantina River and Cooper Creek waterholes in Australia) (V. Bailey, personal communication).

Creation of habitat with flooding results in significant movements in some species. Longfin dace and pupfishes *Cyprinodon* spp. from North America disperse to temporary habitats during flooding (Deacon

& Minckley, 1974) whereas suckers (*Catostomus* and *Pantosteus* spp.) migrate to spawning grounds (Weiss *et al.*, 1998; Douglas & Douglas, 2000). Colorado pikeminnow *Ptychocheilus lucius* migrated about 140 km along the Green River (Colorado River Basin) (Tyus, 1990) and golden perch moved over 1000 km in the Murray–Darling Basin of Australia (Reynolds, 1983). Floods produce other extraordinary movements in Australian fishes. Spangled perch *Leiopotherapon unicolor* swam along 16 km of wheel ruts in six hours (Shipway, 1947), a feat earning it the local reputation of appearing as rains of fishes (Wager & Unmack, 2000). Sometimes dispersal during flooding leads to desiccation and death. Small spates or large floods devastate larval fishes by removing them from suitable habitat to ephemeral downstream reaches, where they die (Deacon & Minckley, 1974).

Dams, diversions and floodplain developments have significantly reduced and affected native fish populations in desert rivers by altering flow regimes (Minckley, 1991; Contreras & Lozano, 1994; Thomas, 1995; Gehrke *et al.*, 1995; Lemly *et al.*, 2000; Chapter 8, this volume). Other contributory impacts include overfishing, pollution and grazing pressure (Robertson & Rowling, 2001). In many desert rivers, introduced species may dominate native species (Fig. 7.4). Overgrazing denudes the watershed, resulting in high sedimentation rates, as well as decreasing riparian vegetation. Native fish populations in North America have declined significantly (Minckley & Deacon, 1991), sometimes to extinction (Williams *et al.*, 1985). For example, the lower Colorado River from below Lake Havasu to the Gulf of California (c. 400 km) has no native fish species and is now populated by 30–40 introduced fish species (Minckley, 1991). Most habitats within the Colorado River Basin have two to three times more introduced fish species, which also dominate in abundance relative to native fishes. Native fish species have declined significantly in the Murray–Darling Basin, with some lowland rivers having only 20% native species compared with exotics (Gehrke & Harris, 2001). Similar shifts in composition have occurred in Iran (Coad, 1980; Coad & Abdoli, 1993), Israel (Goren & Ortal, 1999) and Saudi Arabia (Al Kahem & Behnke, 1983; Ross, 1985; Krupp *et al.*, 1990). River regulation (altered flows, migration barriers, floodplain alienation) has considerably affected native fish populations in Australia (Gehrke *et al.*, 1995), along with cold-water pollution, overfishing, exotic species and pesticides; exotic species may not be favoured by natural flooding patterns (Puckridge *et al.*, 2000; Bunn & Arthington, 2002).

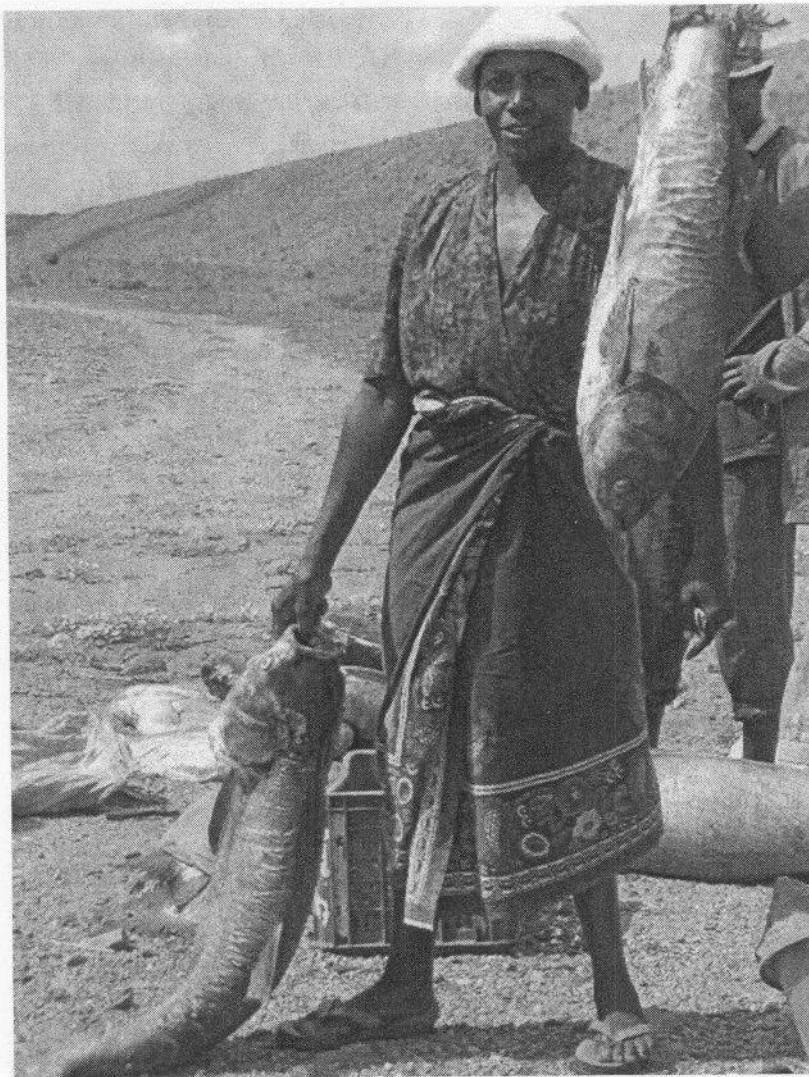


Figure 7.4. Exotic species such as silver carp *Hypophthalmichthys molitrix* from the Massingir reservoir on the Elephants River, Mozambique, often establish with river regulation and the building of dams on desert rivers. They may be an important source of protein for local people but may also affect the ecology of native fish species (Photo M. Wishart).

Some exotic fish species were introduced into rivers whereas others were probably accidental introductions but have been favoured by river regulation, which has generally reduced flow variability (Gehrke *et al.*, 1995). Several examples from North America demonstrate that adult native fish species were unaffected by extreme flooding, but introduced species were extirpated or severely reduced in numbers (Deacon & Minckley, 1974; Meffe & Minckley, 1987; Minckley & Meffe,

1987). In the Guadiana River of Spain, exotic species numbers increased with river channelisation whereas native species numbers declined (Corbacho & Sánchez, 2001). Incidence of pathogens and fish disease could conceivably increase with regulation, increased nutrients and pesticides. Such global effects on desert fishes will continue to affect their survival because of the burgeoning human population in deserts and their adjacent regions and their expanding need for freshwater (Minckley & Deacon, 1991; Chapters 8 and 11, this volume).

AMPHIBIANS

Amphibians are the least likely of vertebrates to be regarded as denizens of the desert. Most experience high rates of evaporative loss, as their skin typically lacks structures to retard water loss. A boundary layer of water vapour around the skin of most amphibians resists evaporation (Spotila & Berman, 1976). Amphibian urine is usually dilute, seldom exceeding osmotic concentration of the body fluids (Adolph, 1927). Amphibian life histories are biphasal with tadpoles dependent on free-standing water for their development. So amphibians cannot achieve the degree of independence of free-standing water possible for other vertebrates, apart from fishes.

Despite these limiting attributes, many of the world's frog species (Table 7.3) successfully inhabit arid regions of the world, reliant on the flows of rivers and streams that fill wetlands. Australian frogs of the genera *Cyclorana* (12 species, 8 of which occur in arid regions) and *Neobatrachus* (9 species, all from dry or arid regions) are well known for their physiological and behavioural adaptation to desert existence (Main, 1968). The spadefoot toads of North America (2 genera, 7 species, all arid-adapted) occupy extremely arid regions including the Sonoran Desert (Mayhew, 1968); the deserts of Africa and South America each have a distinctive frog fauna (Poynton, 1964; Blair, 1976). Desert frogs live on floodplains and in permanent and ephemeral pools of desert rivers, usually not far from water (Predavec & Dickman, 1993). There are no truly desert forms of salamanders or urodeles (Heatwole, 1984).

Arid-adapted frogs cope with unpredictability in the availability of water with different morphological, physiological and behavioural adaptations, varying among species in relation to each one's own unique solution to the problems of desert living (van Beurden, 1982). Morphological, physiological and behavioural convergence across disparate

Table 7.3. Diversity of habits for examples of reptile and amphibian species in Africa (AF), Australia (AU), North America (NA) and South America (SA) dependent or partly dependent on aquatic habitats created by desert rivers

Class	Family	Species	Habits
Amphibia	Bufonidae (toads)	<i>Bufo alvarius</i> (NA)	Toads spend most of the year underground, in burrows they have dug themselves or abandoned rodent burrows. Active after rain, they breed in ephemeral pools
		<i>Crinia deserticola</i> (AU)	Inhabits creek beds, soaks and claypans associated with broad river channels throughout its range
	Myobatrachidae (southern ground frogs)	<i>Limnodynastes spenceri</i> (AU)	A burrowing frog found in sandy beds of ephemeral streams in arid regions
		<i>Limnodynastes tasmaniensis</i> (AU)	Found under logs and stones at the edge of permanent and semi-permanent waterholes
	Hylidae (tree frogs)	<i>Neobatrachus</i> sp. (AU)	Species of burrowing frogs inhabiting arid regions where they are active above ground only after rain; many breed in flooded claypans
		<i>Notaden nichollsi</i> (AU)	
		<i>Uperoleia micromeles</i> (AU)	
		<i>Cyclorana</i> spp. (AU)	A group of stout burrowing frogs from Australia showing remarkable convergence in body form to the burrowing ground frogs of the Myobatrachidae. Cocoons. Active only after rain
	Hyla	<i>Litoria rubella</i> (AU)	Seeks refuge in trees and shrubs beside permanent and semi-permanent waterholes in central Australia
		<i>Hyla cadavarina</i> (NA)	Associated with oases in desert regions. Seeks refuge in crevasses close to water
		<i>H. regilla</i> (NA)	
		<i>H. arenicolor</i> (NA)	Restricted to riparian areas in rocky canyons in desert grassland regions of Colorado, where it is typically found along streams among medium to large boulders

Table 7.3. (cont.)

Class	Family	Species	Habits
	Hyperoliidae (African reed frogs)	<i>Pternohyala fodiens</i> (NA)	A burrowing species that forms a cocoon from shed skin layers. Also uses the casque on its head to block the opening to its burrow.
		<i>Phyllomedusa sauvagii</i> (SA)	Adapted to its arid environment, this frog coats itself with a waxy secretion to keep in moisture. It also expels its urine in the form of semi-solid urates
		<i>Hyperolius</i> spp. (AF),	Extremely low rates of evaporative water loss allow them to persist in arid regions
		<i>Chiromantis</i> spp. (AF)	
	Pelobatidae (spadefoot toads)	<i>Scaphiopus</i> spp. (NA)	Burrowing frogs active only after rain. Breed in ephemeral ponds
		<i>Spea</i> spp. (NA)	
	Reptilia	<i>Emydura macquarii emmotti</i> (AU)	Occupies permanent waterholes in the channel country of arid central Australia
		<i>Chelodina steindachneri</i> (AU)	Occupies permanent and ephemeral waters of arid western Australia, surviving the periods of no surface water by aestivating
	Emydidae (pond turtles)	<i>Clemmys marmorata</i> (NA)	Relict populations occupying man-made and natural ponds in the floodplain of the Mojave River, of the central Mojave Desert, California
		<i>Kinosternon sonoriense</i> (NA)	Occupies permanent and semi-permanent bodies of water in the Sonoran Desert, aestivating during periods when surface water is absent
	Crocodilidae (crocodiles and relatives)	<i>Crocodylus niloticus</i> (AF)	Occupies permanent and semi-permanent bodies of water in the Sahara Desert, aestivating during periods when surface water is absent. Also in the Nile River and waterbodies of its floodplain, in reaches that flow through desert

lineages are common, as for example in striking convergences of the myobatrachid and hylid desert frogs of Australia. Until relatively recently, the genus *Cyclorana* was thought to belong to the Myobatrachidae because its true affinity with the Hylidae was obscured by convergence in body form and external characteristics for burrowing (Tyler, 1978).

Some species, such as *Hyla cadaverina* of the Colorado Desert (McClanahan *et al.*, 1994), survive in permanent seeps or waterholes. With free-standing water readily available, they control body temperatures through evaporative cooling to overcome the oppressive heat of the desert. Arboreal forms in the genus *Phyllomedusa* depart greatly from the norm and live away from water by producing uric acid and by using their feet to smear waterproofing lipids produced by specialised glands over their bodies (Blaycock *et al.*, 1976; Shoemaker, 1988).

Despite these notable exceptions, most desert-adapted frogs are inactive when free water is unavailable. Some species survive the dry times in crevices, sealing the entrance with part of their bodies. The tree frog *Corythomantis greeningi* from semi-arid regions of Brazil has a casque-like head: it is flat and rough with dermal bony elements near the skull (Jared *et al.*, 1999). The frog blocks its retreat with its casque-like head protecting it from desiccation and predation (Seibert *et al.*, 1976).

Many other desert-adapted species escape desiccation by burrowing beneath the soil. These burrowing frogs commonly have a globose body form, short stout limbs, spade-like metatarsal tubercles and a urinary bladder of large capacity. The North American desert spadefoot *Scaphiopus couchii* spends up to 10 months of the year in a deep burrow, buffered from desiccation and high temperature (McClanahan, 1967), and only emerges after heavy rainfall (Dimmitt & Ruibal, 1980). The Australian water-holding frog *Cyclorana platycephalus* can be inactive for many years, conserving water by enveloping its body in an epidermal cocoon while buried. Three genera of Australian frog (Lee & Mercer, 1967), two genera of South American frog and one genus of North American frog (McClanahan, 1967) have cocoons. In Australian frogs, cocoons can reduce evaporative loss to as low as 6% of that of inactive animals without cocoons (Lee & Mercer, 1967).

Periods of activity for desert frogs are brief and unpredictable, usually after heavy rains that produce free-standing water for breeding when a flush of insect activity (Predavec & Dickman, 1993) and later plant growth are available for adults and young frogs. Some desert frogs may be able to predict rain, emerging eight hours before rain began in

the Australian desert (Predavec & Dickman, 1993). Emerging frogs rapidly take up water with specialised seat patches, highly permeable regions where the skin is thin, highly vascularised (Roth, 1973) and responsive to hormonal activation (Baldwin, 1974). Desert frogs have short, opportunistic, explosive mating systems (Sullivan, 1989) and rapid tadpole development (taking as little as 8 days to complete in *Scaphiopus couchii* (Newman, 1989)). There is also flexible timing of metamorphosis when water levels drop or tadpole densities increase (Newman, 1994), and young can sometimes burrow and survive for limited periods. For example, adults of the water-holding frog *Cyclorana platycephalus* emerge after heavy summer rains and mate on the evening of emergence. Eggs are laid in claypans or temporary ponds. Development is extremely rapid and the emergent froglet is relatively large, well endowed with abdominal fat reserves and ready to burrow (van Beurden, 1982). Such activity produces high densities, reaching more than 2000 g ha⁻¹ in some Australian desert frogs (Predavec & Dickman, 1993). These features are directly related to the unpredictability in the timing and duration of flooding and consequent availability of food for adult and tadpole survival.

Amphibians are surprisingly capable of inhabiting desert regions and many occupy the floodplains, and permanent and ephemeral pools of desert rivers. We found no studies that showed that the life history of a frog was driven by the dynamics of the desert river itself. Local rainfall events often produce widespread flooding (Kingsford *et al.*, 1999) that may coincide with flood events from upstream, so frog activity and flooding often coincide. However, their activities seem primarily stimulated by local rainfall, rather than flow patterns of desert rivers and widespread inundation. This may be due to failure of frogs to take advantage of the opportunities brought by episodic inundation of the desert landscape by flooded rivers or simply a knowledge gap for future research.

BIRDS

Of the more than 9000 species of bird in the world (Perrins, 1990), two main ecological groups depend on desert rivers and their habitats: waterbirds and 'terrestrial' bird species whose life cycles depend on aquatic systems (Table 7.4). Terrestrial bird species all require water to drink, even if only occasionally (Young, 1981), and many depend on other resources of aquatic habitats, such as food or nesting materials.

Table 7.4. Major bird groups of the world dependent or partly dependent on aquatic habitats created by desert rivers, and their habits

Group	Common names	Taxonomic group	No. ^a	Habits in desert river systems
Aquatic	Grebes	Podicipediformes	14	Almost completely aquatic, feeding on fishes and invertebrates
	Pelicans	Pelecaniformes	6	Almost completely aquatic, feeding on fishes by scooping fishes into their gular pouch. They breed on islands
	Cormorants and darters		11	Almost completely aquatic, feeding mostly on fishes and large crustaceans, capturing prey underwater. Breeding on islands and trees bordering wetlands
	Hérons and bitterns	Ciconiiformes	61	Long-legged wading birds that feed in shallows around edge of wetlands
	Storks		18	Large long-legged and long-necked birds, generally with heavy bills. Feed on crustaceans, fishes and amphibians and nest in trees, cliffs or buildings
	Spoonbills and ibis		31	Feed on fishes, amphibia crustaceans, insects in and around edges of wetlands or terrestrial areas. They breed in large colonies on platforms made from vegetation

Table 7.4. (cont.)

Group	Common names	Taxonomic group	No. ^a	Habits in desert river systems
	Flamingos		4	Long-legged wading birds with webbed feet. They sieve microscopic plants and animals from alkaline lakes and lagoons
	Ducks, geese and swans	Anseriformes	147	Large group of waterbirds with wide variety of habits from herbivores to invertebrate- and fish-eaters that use the range of wetland habitats from the terrestrial (e.g. geese) to almost completely aquatic (e.g. diving ducks). Nesting is variable
	Screamers		3	Long-legged and with part webbed feet; mainly herbivorous birds that nest close to water
	Cranes	Gruiformes	15	Large, long-legged omnivorous birds that live around water but are capable of feeding in terrestrial habitats. They usually nest on aquatic vegetation in shallow water
	Rails		129	Not all are aquatic species. Small cryptic birds. Some have lobed feet (e.g. coots). They nest on aquatic vegetation
	Finfoots		3	Aquatic birds with long heads and necks, lobed toes and stiff tail

Table 7.4. (cont.)

Group	Common names	Taxonomic group	No. ^a	Habits in desert river systems
	Plovers, jacanas, avocets, stilts, sandpipers, terns, gulls and skimmers	Charadriiformes	245	A diverse group of birds that includes small wading birds that usually feed along the edges of aquatic habitats, jacanas that seldom venture from the vegetation in the middle of wetlands, and gulls, terns and skimmers that usually forage from the air
Terrestrial	Kingfishers	Coraciiformes	87	Many species feed and breed near aquatic habitats, relying on aquatic animals (e.g. fishes) for food. They nest in holes in trees, banks of rivers or termite holes
	Eagles, kites and hawks	Falconiformes	286	A small number of these species (e.g. fish eagles, ospreys, harriers) prey on aquatic species and nest in trees close to water
	Bee-eaters	Coraciiformes	24	Some species feed near habitats of desert rivers and nest in large colonies in river banks
	Parrotbills and reed warblers	Passeriformes	49	Many occupy dense reedbeds around swamps, feeding on insects in the wetlands and building nests within the vegetation

^a Data from Perrins (1990), but not all species found on desert rivers. Gaviiformes (divers and loons, four species) are excluded because their wetland habitats are not usually in desert regions.



Figure 7.5. Large concentrations of waterbirds collect on inland lakes in Australia, such as Lake Wyara. Their numbers fluctuate with regional and continental availability of wetland habitats, which are a response to floods and droughts of desert rivers (Photo R. T. Kingsford).

Among desert birds, waterbirds are often the most conspicuous and abundant (Fig. 7.5) and they tend to concentrate in the lower parts of desert aquatic habitats: the lakes, floodplains, swamps, river channels and estuaries (Turpie, 1995; Kingsford *et al.*, 1999) (Table 7.1, Fig. 7.1). Of all the taxonomic groups of waterbirds, only loons (Gaviiformes) are not found in desert regions. Specialised body forms and feeding structures allow waterbirds to occupy specific aquatic habitats (e.g. deep water areas, shallows, reed beds, floodplains) on a desert river, feeding on a wide range of different foods: invertebrates (ducks, flamingos), plants (geese and swans), fishes and frogs (storks, ibis, egrets). Bills vary enormously. Skimmers *Rynchops* spp. capture small fish and crustaceans while flying close to the water's surface by snapping their long flattened lower mandible, trailing in the water, shut against the short round upper mandible. Whale-headed storks *Balaeniceps rex* catch lungfish and other prey with their enormous bills (Table 7.4). Flamingos *Phoenicopterus* spp. use specialised bills to sieve microscopic biota. Ubiquitous pelicans are piscivores and have a large bill with a sack-like pouch to

temporarily store prey. The specific habits of waterbirds also vary. Some species seldom venture onto land (e.g. grebes, diving ducks *Aythya* spp.) whereas others spend most of their time either around the edge of wetlands (egrets, herons) or often on land adjacent to waterbodies (geese, ibis).

'Terrestrial' bird species dependent on aquatic habitats comprise three taxonomic groups (Table 7.4). There are specialist birds of prey that are totally dependent on aquatic habitats (e.g. African fish eagle *Haliaeetus vocifer*, hammerkop *Scopus umbretta*, (Fig. 7.2) but some falcons and hawks also collect around wetlands in arid regions because of the abundance of waterbirds, fishes and carrion. During aerial surveys of Cooper Creek in Australia, concentrations of hundreds of wedge-tailed eagles *Aquila audax*, black kites *Milvus migrans* and whistling kites *Haliastur sphenurus* were recorded along the edges of the river and its freshwater wetlands (R. T. Kingsford, personal observations). Some species of bee-eater (e.g. carmine bee-eater *Merops nubicus*) nest in large colonies in the banks of desert rivers, and others forage near desert rivers. Parrotbills and reed warblers *Acrocephalus* spp. are passerines primarily dependent on vegetation along desert rivers, particularly wetland areas such as swamps and lakes (Table 7.4).

Birds are the best equipped of all vertebrates to exploit rapidly changing resources because they can fly to or from rivers during 'boom' and 'bust' periods (Schodde, 1982). Many aquatic and terrestrial bird species use the aquatic habitats of desert rivers only at certain times. In particular, migratory species (e.g. white stork *Ciconia ciconia*) breed during the northern hemisphere spring and then fly south during the winter months to feed in the habitats of desert rivers. Seasons may be predictable but temporal and spatial habitats on desert rivers are usually not (Roshier *et al.*, 2001a), resulting in nomadic movements (Roshier & Reid, 2003). Other species, particularly colonially breeding waterbird species, return to where they were hatched to breed. For example, flamingos breed in a few locations (e.g. Lake Baringo in eastern Africa), but feed at others (Vareschi, 1978). Although locations for breeding egrets, ibis and herons are predictable, they only nest following unpredictable widespread flooding of desert rivers in Australia (Kingsford & Johnson, 1998; Leslie, 2001). Most other Australian waterbirds also breed in response to flooding, particularly in desert regions (Kingsford & Norman, 2002). Terrestrial birds also have a rapid breeding response, following flooding and rainfall (Schodde, 1982; Davies, 1984; Lloyd, 1999).

Waterbirds in desert regions capitalise on 'boom' periods when rivers are in flood, creating considerable habitat (Kingsford *et al.*, 1999; Herremans, 1999). Temporary and saline habitats appear to be more productive in terms of density, numbers of species and abundance of waterbirds than those perennially flooded (Fig. 7.5) (Kingsford & Porter, 1993; Kingsford *et al.*, 2004). For waterbirds, movements extend beyond river catchments to continents and beyond (Haig *et al.*, 1998; Roshier *et al.*, 2001b, 2002; Roshier & Reid, 2003). During dry periods, waterbirds concentrate in remaining habitats (Kingsford, 1996; Schlatter *et al.*, 2002). Unpredictable wetland habitats (Roshier *et al.*, 2001a) produce variable movement patterns for desert waterbirds (Roshier *et al.*, 2002), considerably more than is found in movements of northern hemisphere species (Kingsford & Norman, 2002).

REPTILES

Many reptile species are aquatic, semi-aquatic or derive a substantial proportion of their foods from aquatic ecosystems (Table 7.3). They include the freshwater and marine turtles, the crocodilians, lizards of several families including the Agamidae, Iguanidae and Varanidae, and numerous freshwater and marine snake species. Relatively few aquatic species live in desert regions, and most of those that do survive as either relict populations from historically wet times, or with specific adaptations for desert life.

The western pond turtle *Clemmys marmorata* occupies constructed and natural ponds in the floodplain of the Mojave River of the Mojave Desert, California. Their life history differs little from populations in the moister coastal regions, with no identifiable adaptations to desert living. They are probably relict populations from the Pleistocene (Lovich & Meyer, 2002), with tenuous long-term prospects because of drawdown of their habitat for water resource development.

Populations of the Nile crocodile *Crocodylus niloticus* (Fig. 7.2) in Saharan Africa seem to share similar tenuous prospects (de Smet, 1998) but for different reasons. Middle Holocene remains and rock paintings indicate that the crocodiles used to occur across the Sahara. Some populations persist as relicts of this more widespread distribution. A few specimens survive in pools in a few river canyons of the Ennedi plateau of northern Chad. Another relict population, in the Tagant hills of Mauritania, appears to have become locally extinct as recently as 1996 (de Smet, 1998). Nile crocodiles also inhabit two types of wetland

on the periphery of the Sahara (Mayell, 2002): lowland wetlands and a type of wetland known as a guelta. A guelta is formed when rain, or sometimes underground springs, forms a pool of water in a depression of a rocky plateau. Lowland wetlands in Mauritania are formed when rainwater collects in clay-lined depressions in otherwise dryland conditions. In both cases, no permanent water exists in the vicinity, and the crocodiles survive dry periods by aestivating in crevasses and burrows. Unlike the Western pond turtle, these crocodile populations appear to be showing behavioural adaptation to desert life.

The Sonoran mud turtle *Kinosternon sonoriense* occupies remote arid mountain ranges in southern Arizona, New Mexico (USA), and northern Sonora (Mexico). It lives in permanent bodies of water but can also survive dry periods by aestivating (Peterson & Stone, 2000). In Australia, the helmet-shell turtle *Chelodina steindachneri* lives almost entirely within desert regions in creeks and rivers that flow only after infrequent and sporadic heavy rain (Burbidge, 1967). During dry periods of months or even years when there is no water, this species also aestivates, with physiological adaptations for surviving these dry periods. These include low rates of evaporative water loss, tolerance of high temperatures, efficient conversion of ammonia to urates, and capacity to store water in its urinary bladder (Burbidge, 1967).

Our knowledge of reptile ecology in relation to disturbance regimes of desert rivers is relatively poor, but valuable insights are coming from turtle research on Cooper Creek in Australia. This desert river is an extensive system of anastomosing channels, discharging into the inland Lake Eyre (Kingsford *et al.*, 1999). Local rainfall and rain depressions in the catchment, driven by summer tropical monsoons and aseasonal cycles of the El Niño – Southern Oscillation (Puckridge *et al.*, 2000), produce widespread flooding of thousands of hectares (Kingsford *et al.*, 1999; Roshier *et al.*, 2001a). Most of the time, the system is dry (Puckridge *et al.*, 2000) but with many almost permanent waterholes in its mid sections (Knighton & Nanson, 1994). Turtles have three options in this unpredictable environment. They can live in temporary habitats until dry periods come and then move to remaining waters, always live in the permanent waterholes, or live underground in cavities and undercut banks until the next flood. The eastern snake-necked turtle *Chelodina longicollis* is a freshwater turtle that moves overland between ephemeral and permanent waters (Kennett & Georges, 1990, 1995). Although established in the headwaters of Cooper Creek, it has not extended its range into the drier parts of the river, presumably

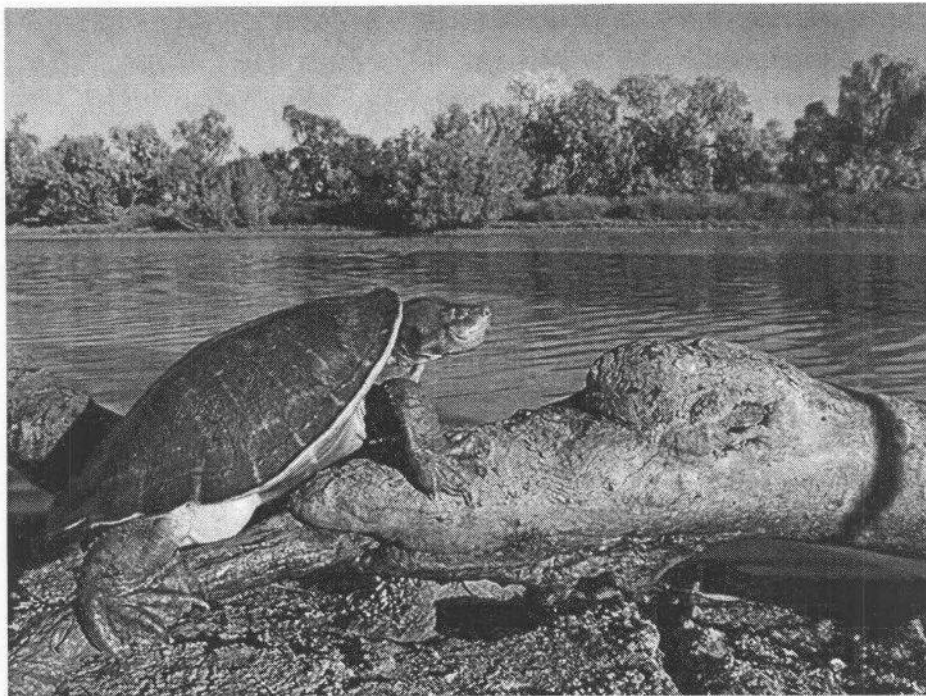


Figure 7.6. The Cooper Creek turtle *Emydura macquarii emmotti* lives in semi-permanent and permanent waterholes of Cooper Creek, such as this one, and the Diamantina River in Australia, seldom venturing overland. During 'boom' flood periods they move onto the floodplain to feed but then retreat to the waterholes when dry 'bust' periods follow (Photo A. Emmott).

because it cannot move between habitats. Large spatial scales of hundreds of kilometres and long temporal scale of decades of inhospitable desert between temporary and permanent waters are too great a barrier for survival.

Instead, Cooper Creek and the nearby Diamantina River are occupied by another river turtle, the Cooper Creek turtle *Emydura macquarii emmotti* (Georges & Adams, 1996) (Fig. 7.6). It does not possess the specific adaptations to the vicissitudes of life in ephemeral habitats of *Chelodina* (Burbidge, 1967; Kennett & Georges, 1990, 1995; Kennett & Christian, 1994). It seldom moves overland in search of water or aestivates during dry periods. Instead this turtle is tied to permanent and semi-permanent waterholes of the channel country on the Diamantina River and Cooper Creek (Fig. 7.6). It capitalises on the 'boom-bust' cycle of resource availability (White, 2002). During infrequent flooding, the turtles move onto the floodplain to feed, retreating with the receding floodwaters to

the discrete permanent waterbodies during 'bust' or dry periods. There is usually a lag in the 'boom' period for the turtles that feed on the great concentrations of dead and dying fishes in the waterholes for months after flooding. Extraordinarily high population densities of turtles live in these permanent waterholes, sustained by the 'boom' periods and persisting through the dry 'bust' periods by virtue of a low metabolic rate (compared with that of birds and mammals) and longevity (up to 80 years). Their ability to survive periods of low production in high population densities is an important ingredient in their success.

None of the waterholes of the channel country is truly permanent, although they may appear to be so on human timeframes. Drying occurs and causes catastrophic mortality (Cann, 1998) with local population extinction. Although the turtles show high site fidelity, regional persistence probably relies on a pattern of local extinction and reinvansion on a timescale of centuries, following the geomorphic scales of the river (Knighton & Nanson, 1994, 2000). The occupation of both 'permanent' and semi-permanent waterholes is also important to their long-term persistence in desert regions.

In summary, aquatic reptiles persist in desert regions through three primary strategies. First, they occupy permanent waterbodies (e.g. waterholes, lakes, rivers, swamps), often as relictual populations. Second, when extensive inundation of the desert landscape occurs sporadically, aquatic reptiles disperse to the newly created habitats. Third, some turtles can also aestivate for months or even years to survive 'bust' or dry periods.

MAMMALS

Relatively few mammals are entirely aquatic compared with other vertebrates (Table 7.5). Mammals that spend most of their lives in water (Table 7.5) are well equipped for such an existence. Apart from completely aquatic river dolphins, other aquatic mammals sometimes move on land (Table 7.5) as exemplified by the hippopotamus *Hippopotamus amphibius*, which feeds on land at night and spends the day in the water. Many aquatic mammals have partly or fully webbed feet (e.g. otters, water rat). In contrast the sitatunga, an antelope of terrestrial origin, is able to move over the unstable aquatic vegetation of African swamps, supported by splayed hooves. Most aquatic mammals also have sensory organs near the top of their heads (e.g. hippopotamus, capybara,

Table 7.5. *Habits of major mammal groups of the world dependent or partly dependent on aquatic habitats created by desert rivers*

Group	Common names	Taxonomic group	No.	Habits in desert river systems
Aquatic	Platypus	Monotremata	1	Almost completely aquatic, feeding on invertebrates and primarily confined to mesic parts of desert rivers
	River dolphins		5	Two species of river dolphin live in parts of desert rivers: the Indus dolphin <i>Platanista minor</i> and the Ganges dolphin <i>P. gangetica</i> .
	Rodents	Rodentia	<30	Many rodent species live primarily in water. They have nostrils, eyes and ears near the top of their heads and many have partially or fully webbed feet and flattened tails for an aquatic life. Species include the water rat <i>Hydromys chrysogaster</i> , South American water rat <i>Nectomys</i> , coypu <i>Mycogaster coypus</i> , capybara <i>Hydrochaeris hydrochaeris</i> , marsh rats (<i>Holochilus</i> spp.) and swamp rats (<i>Malcomys</i> spp.)
	Otters	Carnivora	13	These species are primarily aquatic with webbed feet, short fur, small ears and eyes on the top of their heads. They feed on fishes and crustaceans and insects in desert rivers. Species include the Cape clawless otter <i>Aonyx capensis</i> , smooth-coated otter <i>Lutrogale perspicillata</i> and spot-necked otter <i>Lutra maculicollis</i>

Table 7.5. (cont.)

Group	Common names	Taxonomic group	No.	Habits in desert river systems
	Hippopotamus	Artiodactyla	2	The hippopotamus <i>Hippopotamus amphibius</i> has large lungs and ears, eyes and nose on top of the head, muscles for closing eyes and ears under water, and broad muzzle. Daytime is spent in water; nocturnal feeding on floodplains
	Spiral-horned antelope		9	Some species live within swamps and floodplains and include sitatunga <i>Tragelaphus spekeii</i> , a species with specialist splayed hooves to support its weight in swamps, nyala <i>T. angasii</i> and species of reedbuck <i>Redunca arundinum</i> , <i>R. redunca</i>
	Grazing antelope		23	Some species live primarily on floodplains and include lechwe <i>Kobus leche</i> , <i>K. megaceros</i> and waterbuck <i>K. ellipsiprymnus</i>
	Insectivores	Insectivora	5	Specialist species (aquatic tenrec <i>Limnogale mergulus</i> , giant otter shrew <i>Potamogale velos</i>) are adapted for an aquatic existence with elongated body form and eyes and ears on top of a flattened head
Terrestrial	Bats	Chiroptera	900	Some species use riparian areas and aquatic area for feeding (e.g. large slit-faced bat <i>Nycteris grandis</i>)
	Lions	Carnivora	1	Primarily terrestrial but prey on herbivores around waterholes and wetlands

Table 7.5. (cont.)

Group	Common names	Taxonomic group	No.	Habits in desert river systems
	Humans	Primates	1	Many humans live close to water in desert regions, catching fish and using floodplain plants
	Elephants	Proboscidea	2	Elephants <i>Loxodonta africana</i> require considerable water and during the dry times may dig for water in dry river beds
	Tapir	Perissodactyla	4	Frequently found in rivers and lakes, where they take refuge from predators. Mostly in mesic areas of desert rivers
	Rhinoceros		5	Often found close to water; they use waterholes for wallowing and caking their skin with mud to deter parasites
	Buffalo	Artiodactyla	2	Some African buffalo <i>Syncerus caffer</i> spend much of their time on the floodplains and wetlands of desert rivers; water buffalo, as their name implies, live primarily in wetlands of desert rivers

long-haired rat *Rattus villosissimus*, thick-tailed opossum *Lutreolina crassicaudata*), allowing them to look out for prey or predators while mostly submerged. Many of them also swim well, with streamlined bodies propelled by flattened tails that also sometimes act as rudders.

Although few aquatic mammals depend entirely on desert rivers (Table 7.5), most mammals have to drink from a river or wetland. There are a few exceptions that can last for periods without water (oryx *Oryx gazella*, bilby *Macrotis lagotis*). Desert rivers and their dependent habitats are the focus for interactions between many mammal species and other vertebrates (Fig. 7.1). In the upper catchment of a desert river, the



Figure 7.7. Terrestrial species depend on rivers and wetlands in desert regions for their water, sometimes needing to travel up to 200 km to find water during dry periods. African elephants bathe and drink from the Ewaso Ngiro River, Kenya (Photo H. Grant).

riparian corridor (Malanson, 1993) and water attract mammals. Forest-dwelling mammals come to drink or feed in the riparian vegetation (Table 7.1). Much of our knowledge of interactions between mammals, other than humans, and rivers comes from research from northern latitude catchments and the importance of the riparian corridors (Nilsson & Dynesius, 1994). Otters, aquatic rodents and platypus, with specialist aquatic adaptations, are among the few aquatic mammal species, living in channels of desert rivers in the upper catchment (Table 7.1), where they feed on invertebrates and fishes.

In the mid-section of a river, increasing aridity brings many mammals to the river to drink, bathe or feed. For example, African elephants require 80–160 l of fluid a day (Macdonald, 2001) and either live near permanent water or travel up to 200 km to reach water during dry periods (Fig. 7.7) (Verlinden & Gavor, 1998). Large waterholes and a wide channel allow aquatic mammals such as hippopotamus to establish territories (Jacobsen & Kleynhans, 1993). Diversity and abundance of mammals is probably highest in the lowest part of a desert river: the floodplains, terminal lakes and estuaries (Table 7.1; Fig. 7.1). Here, extensive and variable habitats provide considerable opportunity for many species of mammals to survive and reproduce. Reduction of such

areas with river regulation leads to declines in abundance of aquatic mammals (e.g. hippopotamus), which then concentrate in the reduced available habitat (Jacobsen & Kleynhans, 1993; Nilsson & Dynesius, 1994). Even the floodplain feeding habitat of the terrestrial chacma baboon *Papio ursinus* may be reduced (Attwell, 1970).

River channels and deltas provide habitat for aquatic species (e.g. river dolphins, hippopotamus, capybara, tapir) whereas floodplains, wetlands, waterholes and river channels are a magnet for terrestrial mammals that concentrate and interact, drawn by essential requirements of water and abundant food. The lechwe antelope *Kobus leche* lives in large herds on aquatic plants from floodplains or wetlands; the movement patterns and habitat use of African elephants were correlated with proximity to water and nutrient-rich areas during dry periods (Verlinden & Gavor, 1998). Within Australian deserts, the marsupial koala *Phascolarctos cinereus* tends to be found along the main riparian corridors where eucalypts grow largest. The need for mammalian herbivores to drink at waterholes, floodplains, wetlands or river banks produces high encounter rates between predators and prey. Lions *Panthera leo* and crocodiles ambush herbivores near waterholes; smaller mammalian carnivores (e.g. serval cat *Leptailurus serval*) may prey on birds coming to drink. Seasonally abundant vegetation also results in migrations of animals that make difficult river crossings (e.g. wildebeeste *Connochaetes* spp. in Africa), providing nutrients and prey to carnivores and scavengers. Although our knowledge of how disturbance patterns of desert rivers shape the ecology of mammals remains relatively poor, there is accumulating evidence that desert rivers drive the ecology of aquatic mammals and many terrestrial mammals in desert regions.

The availability of food and water meant that humans traditionally concentrated near desert rivers. Material for housing (e.g. reed beds) and food, particularly fishes (Thomas, 1995), are usually available from desert rivers and wetlands. Aboriginal communities in Australia used desert rivers as trade routes (Veth *et al.*, 1990). For the same reason, European colonists built towns on the banks of Australia's desert rivers, near dependable water. Desert rivers were not only utilitarian but also culturally important (e.g. dreamtime stories of Australian aborigines) (Goodall, 1999). Such dependency remains strong in many parts of the world but has been severely changed, with regulation of desert rivers (Lemly *et al.*, 2000; Chapter 8, this book).

Humans are not the only mammals that can change desert rivers. Herbivores exert considerable influence on vegetation patterns,

affecting availability of food for other mammals. African elephants affect vegetation structure and composition on a floodplain and may affect the geomorphology by accessing river banks and wetlands and digging holes in rivers for drinking. Hippopotamus affect spatial flooding to wetlands and lakes in the Okavango Swamp by changing geomorphology and vegetation distribution (McCarthy *et al.*, 1998). The South American coypu similarly affects flooding patterns and has successfully colonised Africa and Europe, affecting flow patterns (MacDonald, 2001).

FLOOD 'BOOMS' AND 'BUSTS' AND EVERYTHING IN BETWEEN

The distribution and abundance of all organisms are dependent on access to sufficient food and water for survival and reproduction. This challenges vertebrates in desert regions because river flows are often so unpredictable (Puckridge *et al.*, 1998; Chapters 1 and 2, this volume). Such hydrological variation creates a range of inundation patterns or habitats from extensive floods, called 'boom' periods, to the bottlenecks or 'bust' periods (Kingsford *et al.*, 1999). These are the extremes, but the 'in-between' floods should not be discounted for their ecological importance. Clusters of floods create productive feeding habitats and recruitment opportunities for some vertebrates, allowing rapid recruitment responses during 'boom' periods (Puckridge *et al.*, 2000). They may be critical in refilling drying waterholes and wetlands that provide refuges for vertebrates (Chapter 4, this volume), priming the aquatic system and ensuring that the next flood creates more habitat (Puckridge *et al.*, 2000).

Floods in desert rivers stimulate tremendous productivity and biological activity. These are the 'boom' times when waterbirds arrive to colonise newly flooded habitats (Roshier *et al.*, 2002; Roshier & Reid, 2003) and plant growth occurs (Bacon *et al.*, 1993). Vegetation within wetlands and floodplains provides extensive areas for herbivorous mammals to forage. Fishes and waterbird populations breed rapidly (Kingsford & Johnson, 1998; Kingsford *et al.*, 1999; Puckridge *et al.*, 2000), providing abundant food for terrestrial vertebrates (e.g. birds of prey).

Inevitable 'bust' periods are more frequent and produce ecological bottlenecks for vertebrates living in the desert aquatic habitats (Table 7.1). As available habitat contracts, many waterbirds 'escape' to other wet habitats, or migrate, but even in birds, many die during 'bust'

periods (Kingsford *et al.*, 1999). Some mammals move away from the area but many remain concentrated around remaining habitat patches (e.g. waterholes). Some desert frogs shut down most of their physiological processes and cocoon themselves underground. Fish populations become more concentrated. For a time, there is an abundance of prey for predators as prey are forced to concentrate in remaining areas. Fish-eating waterbirds collect in considerable numbers around drying lakes and waterholes where there is high density of prey. Similarly, carnivores find easy prey in other vertebrates, unable to stray far from water. The changing boundary between aquatic and terrestrial habitats creates opportunities for plants and animals to colonise. For example, small marsupials and rodents colonise the cracks created as lake beds on desert rivers dry up (Briggs, 1992; Briggs *et al.*, 2000). The Lake Eyre dragon *Ctenophorus maculosus* specifically forages on the dry lake-bed. Such species may be prone to drowning if they cannot escape quickly. In lowland sections of rivers, floods often move reasonably slowly.

Not all aquatic habitats on desert rivers disappear during dry periods. Some (e.g. lakes and waterholes) retain water for years, usually until another flood replenishes their water capacity. These more permanent habitats become island refuges that ensure desert vertebrates can recolonise wetland habitats in the next flood: the colonisation epicentres of desert rivers (Jacobsen & Kleynhans, 1993). Fishes and turtles retreat to these waterholes. For example, the oldest Cooper Creek turtles in central Australia occur only in the deepest waterholes that seldom dry up (Fig. 7.6) (White, 2002).

The two disturbance factors, flooding and drying, shape the quantity, frequency and extent of habitat created by desert rivers. They influence life histories of all aquatic dependent vertebrates in generally predictable ways but habits of desert vertebrates also vary considerably between and within groups. For example, fish-eating waterbirds generally breed later in a flooding regime, compared with other waterbird species, which wait until fish populations reproduce and increase (Kingsford *et al.*, 1999). Different vertebrates also use different parts of a desert river. For example, many desert frogs occupy habitats separated from the main channel of desert rivers, areas primarily reliant on local rainfall for filling of temporary wetlands. But as well as these aquatic vertebrates, we also argue that desert rivers influence the ecology of most terrestrial vertebrate species living in desert regions. These species need to drink mostly from rivers but reliance goes well beyond this physiological dependence. 'Boom' periods on desert rivers allow establishment

of an abundant and diverse biota, supporting complex food webs, including those of terrestrial vertebrates. Stochastic rainfall is a strong determinant of the ecology of desert regions (Stafford Smith & Morton, 1990). Variable flows on desert rivers create and destroy network habitat patches, changing in space and time, for vertebrates. They not only create extensive foraging and recruitment habitats during 'boom' periods but they also concentrate resources during 'bust' periods.

CONCLUSIONS

Vertebrate ecology on desert rivers is considerably different from that on spatially and temporally more predictable rivers in mesic regions of the world. Behaviour of most vertebrates in desert regions is dependent on the counteracting disturbances of flooding and drying. Even most terrestrial vertebrates have their ecology primarily affected by flooding and drying of desert rivers when the habitats created by desert rivers provide abundant food. High species diversity and abundance of vertebrates on riverine habitats in desert regions provides good evidence for the importance of these areas. Only a few vertebrates (some reptiles and mammals) have cut their dependencies on the habitats of desert rivers. Strategies of survival and reproduction among vertebrate groups are remarkably similar. Frogs, fish, turtles and waterbirds all capitalise with extraordinary breeding events during flood periods when there is a relatively short time to complete recruitment. Similarly, during dry periods, the species are able to wait in refugia, whether this is waterholes, lakes or their own cocoons. We argue that the natural hydrological disturbance regimes of desert rivers remain the most important factor shaping the ecology of much of the vertebrate fauna that lives in these areas of the world.

We know relatively little about the interrelationships between vertebrates and desert river systems but there are tantalising pieces of information suggesting that desert rivers without vertebrates would be considerably poorer in diversity and abundance without the 'boom' and 'bust' periods. Some plant and invertebrate species may depend on transportation by birds to colonise different environments (Green *et al.*, 2002). Unlike most other biota (but see vegetation example (Tooth & Nanson, 2000)), vertebrates can change the disturbance patterns of rivers. Large mammals, such as hippopotamus, carve channels through large wetlands, changing flooding and drying patterns of dependent

habitats; large herbivorous mammals may increase the patchiness and suitability of floodplains for other organisms by grazing.

Only humans can completely alter the disturbance patterns of desert rivers with dams and diversion of water, mainly for irrigation (see Lemly *et al.*, 2000; Chapter 8, this volume). Human damage to the ecology of vertebrates at this scale ranks among the most serious conservation problems affecting the world (Chapter 8, this volume).

River regulation and water resource development can remove much of the temporal and spatial complexity and extent of aquatic ecosystems (Chapter 8, this volume). Dry periods become longer and more frequent and flooded habitats shrink in size. What effects would this have on vertebrates in desert rivers and which groups would be most vulnerable? Clearly, such impacts are going to most affect vertebrates unable to withstand extended dry periods and with reduced opportunities to 'bounce back' after breeding events that would be inevitably smaller. If refugia, including lakes, dry up then turtles, waterbirds and fish would have significantly reduced populations. Examples exist where species have become locally extinct (Chapter 8, this volume). For regulated rivers that deliver flow for irrigation or human communities, low flows may also favour exotic species to the detriment of native species that are primarily capable of capitalising on large flood events. Even humans reliant on a subsistence existence are affected, particularly if dependent on fishing and other uses of desert rivers (see Chapter 8, this volume). If waterholes dry up during catastrophic droughts, vertebrates that use rivers primarily for drinking will be just as affected as aquatic dependent vertebrates.

Many questions about the interactions between vertebrates and rivers remain unanswered (Nilsson & Dynesius, 1994), but the reliance of their ecology on disturbance patterns seems clear. The 'boom' and 'bust' periods and everything in between allow many vertebrate species to persist in otherwise hostile environments. When we irrevocably change disturbance patterns, the essential ecology of these unique desert rivers collapses (see Chapter 8, this volume). Natural disturbance patterns of desert rivers are the essence of desert ecosystems and their vertebrates.

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