Glen Canyon Dam: A mixed blessing for mammals, reptiles, and amphibians?

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ABSTRACT

The installation of Glen Canyon Dam has led to many changes in the Colorado River corridor through the Grand Canyon. The effect of the dam on mammals, amphibians, and reptiles is not well understood and poorly studied, but in general is considered positive. A number of animal species, specifically those associated with riparian habitat, have increased in numbers since the dam was closed. Toads, lizards, beaver, small mammals, scavengers, and bighorn sheep are among those species that have probably benefited from the dam's flow regulation. Increases in riparian vegetation, available riparian habitat, insect abundances, and outside food from humans have all contributed to these population changes. The current and future Adaptive Management practices of fluctuating flows and controlled floods aim to decrease riparian vegetation, and may therefore lead to a decrease in habitat and food availability. This could in turn cause a decline in many animal species. However, these declines will probably be small, and are not likely to threaten mammal, amphibian, or reptile populations. Monitoring of these species is essential to ensure that changes in dam operations do not adversely affect their populations.

INTRODUCTION

The effect of Glen Canyon Dam on the fluvial geomorphology and ecology of the Grand Canyon has been a subject of debate for several decades. Today, most people agree that the dam's presence has contributed to the loss and decline of native fishes, drastic changes in the flow regime of the Colorado River through the Grand Canyon, an increase in riparian (especially alien) vegetation, sand bar erosion, and backwater habitat loss. New management practices, which began in the 1990s with the advent of the

Adaptive Management Program, aim to address many of these negative effects of the dam. Current management intends to use controlled floods to improve sand bar habitat, enhance conditions for endangered fish species such as the humpback chub (*Gila cypha*), and reduce encroaching riparian vegetation. Management is also using fluctuating flows in hopes of aggravating select non-native fish and improving the Lee's Ferry tailwater trout sport fishery. However, the Colorado River through the Grand Canyon contains a complex web of species, and current management often fails to recognize the importance of many other species in the ecosystem. Past monitoring of the Colorado River flora and fauna has focused heavily on fish, invertebrates, and birds, while often overlooking other taxa. Current practices also do not emphasize the effects of Glen Canyon Dam on the terrestrial fauna of the Inner Gorge of the Grand Canyon (outside of the endangered Kanab ambersnail and a few bird species), despite the undeniable fact that riparian-associated mammals, reptiles, and amphibians may be affected by fluctuating flows and experimental floods (Fig. 1).

(a) (b)

Figure 1. The beaver (a) and the red-spotted toad (b) are two of the riparian species that may be affected by Adaptive Management's experimental flows (Source: Beaver Wetlands and Wildlife 2002 and www.enature.com/fieldguide).

Due to this shortage of research, there is a general paucity of information on mammal, amphibian, and reptile abundances pre- and post-Glen Canyon dam. The majority of information that is available is largely anecdotal, and focuses on sighting records, which simply inform us about presence or absence. Only a few researchers have attempted to look at abundance or density of these taxa, and all of these studies were done after the dam was closed. No detailed survey data exists for wildlife abundances prior to the dam closure (US Dept. of the Interior 1994). As a result, conclusions about the dam's effect on these taxa remain largely conjectural. However, possible effects on species can be deduced based on changes in habitat and food availability combined with natural history and general ecology principles. For example, many herbivorous species have probably increased since the dam was closed because of the increase in stable riparian vegetation as a food source. The increase in riparian vegetation also increases habitat available for species which require vegetative cover and affects terrestrial insect abundance. Also, an indirect effect of the dam is the increase in river runners and campers, which serve as a food supply for many rodents and omnivorous scavengers.

Possible effects of the current practices of the Adaptive Management Program can also be inferred based on natural history, ecology, and known changes to vegetation, bank structure, and invertebrate populations. Government and independent researchers have done some limited work to look at the effects of Glen Canyon Dam operations on mammals, amphibians, and reptiles. However, a comprehensive analysis of these effects is lacking. With the following discussion, I present a review of the past, present, and future effects of Glen Canyon Dam and its operations on mammals, amphibians, and reptiles.

BACKGROUND

To place the following discussion of amphibians, reptiles, and mammals in context, it is necessary to briefly review the riparian and near-river zones within the Grand Canyon. I will use the description provided by Carothers and Brown (1991) (Fig. 2).

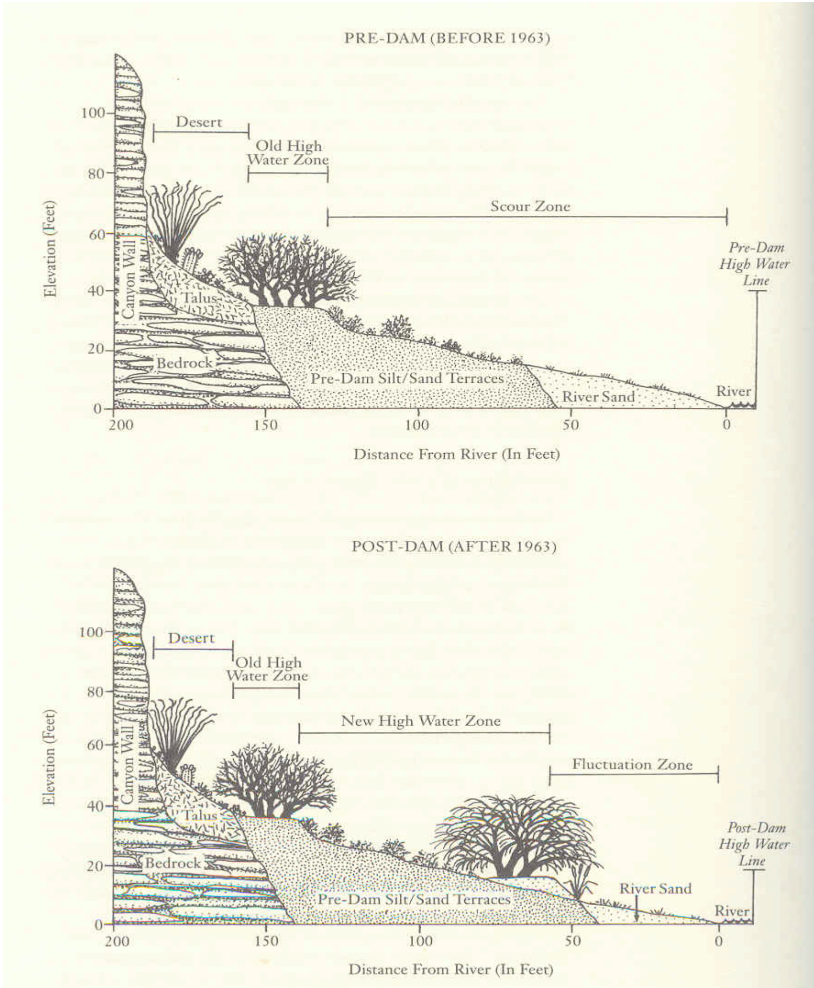


Figure 2. River corridor vegetation zones (Carothers and Brown 1991)

Before the dam, there were three main vegetation zones. Furthest from the river was the desert zone which consisted of non-riparian plant species. The other two zones were the old high water zone (upslope) and the scour zone (downslope), which were divided by the pre-dam (or old) high water line. The old high water zone (OHWZ) was dominated by shrub species which depend on periodic flooding for nutrients and water to reach their roots. The scour zone contained colonizing ephemeral grasses and herbs, along with some willow (*Salix* sp.) and salt cedar (*Tamarisk* sp.) seedlings. These species were periodically (often annually) washed away by floods. Today, as a result of the dam, there are now four zones. The desert zone and OHWZ remain largely unchanged, while the scour zone has been split into the new high water zone (NHWZ—upslope) and the fluctuation zone (downslope). These two zones are divided by the post-dam (or new) high water line. In general, these changes have led to an increase in the amount and stability of riparian vegetation, especially willows and tamarisk, along the river corridor (King 2005, this volume). This increase in vegetation, and the effects that dam operations have on this vegetation, has direct and indirect effects on the wildlife of the corridor.

Other important aspects of the pre- and post-dam river include changes in invertebrate abundance, increased marsh habitat, sand bar erosion, and change in flow regime. These and other issues will be discussed in relation to specific groups and in the context of current adaptive management flows.

AMPHIBIANS

The lives of amphibians are by nature tied to either ephemeral or permanent water sources. Most amphibians require open water (e.g. ponds, streams, puddles, etc.) for the egg and larval stages of their life cycles, and many species remain near or within water during the adult stage as well. The water sources available to amphibians in the Grand Canyon river corridor are slow-moving backwaters or marshes that provide adequate habitat for egg laying and larval development (Miller et al. 1982). Riparian and aquatic vegetation can be important sources of cover for eggs, tadpoles, and adults, and may decrease predation. Also, vegetation and water serve as habitat for insects, which are the main food staple of most amphibians (Stebbins 2003).

In the Grand Canyon there are four amphibian species that use the Colorado River corridor (Table 1). The canyon treefrog (*Hyla arenicolor*) is relegated to the clear water tributaries of the Colorado River only (Miller et al. 1982), and is therefore not focused on in this discussion of Glen Canyon Dam. Of the remaining three species, the red-spotted toad (*Bufo punctatus*) and Woodhouse's toad (*Bufo woodhousii*) are abundant throughout the canyon (Miller et al.1982; Carothers and Brown 1991). Finally, the northern leopard frog (*Rana pipiens*) is known in the canyon from only a few sightings, the first of which was in 1973 (post-dam) at 114.3 km downstream of Lee's Ferry (Tomko 1976). The lack of records suggest that the leopard frog was absent from the canyon before the dam's closure, and sightings since 1973 have remained scarce (Department of Interior 1999).

Species	Pre-Dam	Post-Dam	Habitat	Riparian or	Effect of Glen

	Abundance	Abundance	Preference	Aquatic Dependence	Canyon Dam
Red-spotted toad *Bufo punctatus*	Abundant	Abundant	Riparian, desert scrub	Medium	Positive?
Woodhouse's toad *Bufo woodhousii*	Abundant	Abundant	Riparian	High	Positive?
Canyon treefrog *Hyla arenicolor*	Common	Common	Riparian tributaries	High	Probably none
Northern leopard frog *Rana pipiens*	Absent?	Rare	Riparian with heavily vegetated shoreline	High	Positive?

Table 1. Amphibians. Information from Miller et al. (1982) and Carothers and Brown (1991). Current species names from Stebbins (2003).

KEY TO TABLES:

- *Abundance = along river corridor:*

  Absent<Rare<Uncommon<Common<Abundant
- *Riparian or aquatic dependence:*

  Low—Uses riparian and/or aquatic habitat, but can survive and complete all life cycles without it.

  Medium—Uses riparian and/or aquatic habitat, requires it during some portion of the life cycle, but can persist for periods of time in other habitats.

  High—Prefers riparian and/or aquatic habitat and uses it during some portion of the life cycle.

  Very high—Uses riparian and/or aquatic habitat almost exclusively during all portions of the life cycle and is heavily dependent on it for food, shelter, and/or reproduction.
- *Effect of Glen Canyon Dam:*

  Positive means the dam has led to an increases in numbers

  Negative means the dam has led to a decrease in numbers

  None means no effect

  Unknown means effect is not known

The effects of Glen Canyon Dam on the two toad species have overall been either negligible or positive. Both species are clearly abundant along the river corridor, and seem to heavily occupy the NHWZ. Carothers and Brown (1991) believe that the new river regime has benefited the toads, and state that "These toads can be so abundant in the new high-water zone on summer nights that it is almost impossible to walk through the camp without stepping on one". However, just because the toads are abundant now does not mean that they were not abundant before the dam as well. Both the red-spotted toad and Woodhouse's toad (Fig. 3a) can move away from water when necessary, and therefore have likely been part of the Grand Canyon ecosystem for many years. On the other hand, these toads both depend on insects for food (Miller et al. 1982) and it is believed that the new river regime has promoted an increase in insect abundance in riparian zones (Stevens and Waring 1988). Hence, food availability has probably increased in comparison to pre-dam times. Also, as a result of the dam, there is now more physical space between the desert scrub habitat and the shoreline (Carothers and Brown 1991), which may provide more habitat space and allow for larger populations of toads. A side note is that backwater habitats suitable for egg deposition and tadpole development have decreased due to infill, while marsh habitat has increased. It is likely that both of these habitats are useful for reproduction, and therefore these changes probably cancel each other out. Therefore, based on observations and similar life history traits, it is quite likely that the red-spotted toad and Woodhouse's toad have increased in abundance since closure of the dam.

(a) (b)

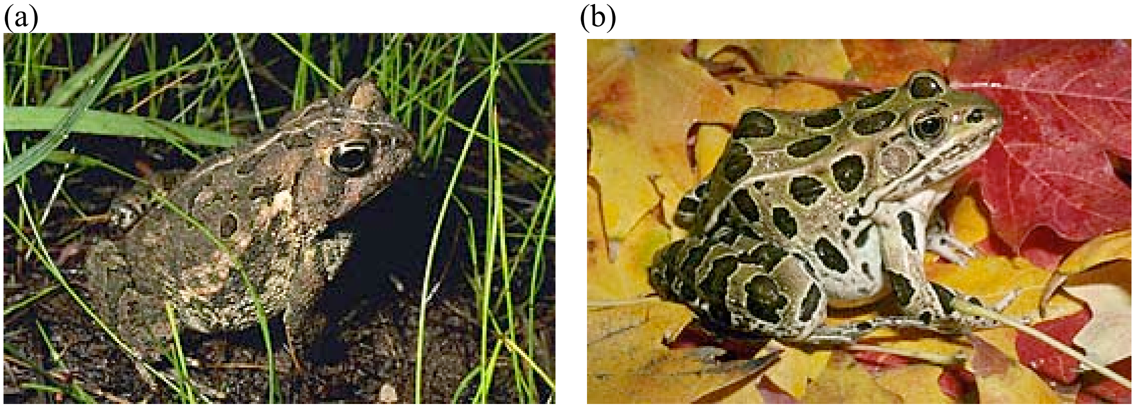


Figure 3. The Woodhouse's toad (a) and northern leopard frog (b) have probably benefited from the dam's presence (Source: www.enature.com/fieldguide).

Similarly, the northern leopard frog (Fig. 3b) may also have benefited from dam closure. This frog was unknown in the Canyon until 1973, and is still considered rare.

Only two individuals have been recorded downstream of Lee's Ferry, and the only known resident population is in Glen Canyon, just below the dam (US Dept. of the Interior 1999). These observations imply that the closure of Glen Canyon Dam may have allowed for leopard frog establishment, although the route by which they arrived in the corridor remains unknown. The change in flow regime, which led to an increase in riparian vegetation and insect abundance, created numerous areas of "frog habitat" that are favorable to leopard frog existence (Tomko 1976, Carothers and Brown 1991, US Dept. of the Interior 1999). Since the leopard frog is highly dependent on riparian vegetation and habitat, and cannot cross desert stretches, it seems unable to traverse the river corridor in large numbers in order to establish new populations. However, Miller et al. (1982) suggests that continued changes in the shoreline (specifically riparian vegetation increases) of the Colorado River may allow for future migration of northern leopard frogs. If riparian vegetation continues to increase as it has in the past 40 years, I agree that an increase in leopard frog numbers and populations is a definite possibility.

Since the dam's operation seems to have previously augmented many amphibians, the current experimental releases and fluctuating flows under the Adaptive Management Program may have a negative impact on these same species. Direct effects of any high flows include disruption of breeding, flushing out egg sacs, and washing away tadpoles from their backwater retreats. Breeding and egg deposition occurs between April and July for the two toad species and the northern leopard frog, while metamorphosis from tadpole to adult probably occurs between June and August (Miller et al. 1982). Therefore, any flooding between April and August is likely to result in some disruption of reproduction and/or mortality of eggs and tadpoles (US Dept. of Interior 2002). However, we should not jump to eliminate any high flows that occur between April and August based on this information. The regulated flow that prevailed post-1963 minimized disturbance of egg deposition and probably allowed for higher survival rates of young than naturally occurred in the pre-dam system. Hence, the current abundance and survival rate of amphibians are likely to be artificial. Furthermore, the species that exist in the river corridor (with the possible exclusion of the northern leopard frog) should be adapted to occasional summer floods that naturally occurred in the Grand Canyon, and therefore their survival should not be dependent on the absence of floods.

Management also aims to decrease riparian vegetation, which may lead to indirect effects on amphibian populations, namely a decrease in available riparian habitat and a decline in insect food supply. While experimental flows may lead to some decrease in amphibian abundance, it is not likely to cause a serious decline in their numbers. However, monitoring of amphibians before and after experimental releases should be undertaken in order to evaluate this hypothesis.

REPTILES

Habitat requirements and diets of reptiles vary widely across species. Within the Grand Canyon river corridor there are both snakes and lizards that have varying levels of dependence on riparian habitat (Table 2). Riparian dependence can be linked to both food and shelter, though in general food resources seem to be the driving force behind changes in lizard and snake populations along the Colorado River (Carothers and Brown 1991). Many of the lizards eat insects, other arthropods, and even aquatic invertebrates; while the snakes in the corridor eat primarily lizards, small mammals, and occasionally birds (Miller et al. 1982). An individual species' level of dependence on the riparian corridor in turn determines how the dam and experimental flows affect it.

Species	**Pre-Dam Abundance**	**Post-Dam Abundance**	**Habitat Preference**	**Riparian Dependence**	**Effect of Glen Canyon Dam**
Western banded gecko *Coleonyx variegatus*	Rare	Rare	Riparian	High	Unknown
Zebra-tailed lizard *Callisaurus draconoides*	Rare	Rare	Sparse vegetation in desert or riparian	Low	Unknown
Western whiptail *Cnemidophorus tigris*	Common/ Abundant	Abundant	Riparian, desert near water	High	Positive?
Great Basin collared lizard *Crotaphytus bicinctores*	Uncommon	Uncommon	Desert scrub, riparian	Low	Probably none
Gila monster *Heloderma suspectum*	Rare	Rare	Riparian, Desert	Medium	Unknown
Common chuckwalla *Sauromalus obesus*	Common	Common	Desert, cliff, riparian	Low	Probably none
Desert spiny lizard *Sceloporus magister*	Common/ Abundant	Abundant	Riparian, cliff and desert near riparian	High	Positive?
Ornate tree lizard *Urosaurus ornatus*	Common/ Abundant	Abundant	Cliff, riparian	High	Positive?
Common side-	Common/	Abundant	Riparian,	High	Positive?

blotched lizard *Uta stansburiana*	Abundant		desert		
Desert horned lizard *Phrynosoma platyrhinos*	Rare	Rare	Desert, riparian	Medium	Probably none
Grand Canyon rattlesnake *Crotalus viridis abyssus*	Common	Common	Desert, riparian	Medium	Positive?
Speckled rattlesnake *Crotalus mitchellii*	Rare	Rare	Desert, riparian	Low	Unknown
Desert night snake *Hypsiglena torquata*	Rare	Rare	Desert, riparian	Medium	Positive?
California kingsnake *Lampropeltis getula californiae*	Common	Common	Desert, riparian	Medium	Positive?
Western blind snake *Leptotyphlops humilis*	Rare?	Rare?	Desert, riparian	Low	Unknown
Red racer *Masticophis flagellum piceus*	Uncommon	Uncommon	Riparian vegetation, desert	Medium	Positive?
Desert striped whipsnake *Masticophis taeniatus taeniatus*	Common	Common	Desert, riparian	Low	Unknown
Mojave patch-nosed snake *Salvadora hexalepis mojavensis*	Uncommon	Uncommon	Desert, riparian	Medium	Positive?
Western ground snake *Sonora semiannulata*	Rare	Rare	Riparian, desert	High	Positive?
Long-nosed snake *Rhinocheilus lecontei*	Rare	Rare	Desert, riparian	Low	Unknown
Western lyre snake *Trimorphodon biscutatus*	Rare	Rare	Desert, riparian	Low	Unknown
Sonoran gopher snake *Pituophis melanoleucus*	Uncommon	Uncommon	Desert, riparian	Low	Unknown
Ringneck snake *Diadophus punctatus*	Rare	Rare	Desert, riparian	Low	Unknown

Table 2. Reptiles. Information from Miller et al. (1982) and Carothers and Brown (1991). Current species names from Stebbins (2003).

Many lizard species in the canyon appear to have benefited from the dam closure, because they heavily use the NHWZ and the fluctuation zone. Warren and Schwalbe (1988) found that lizard abundance and densities were greater in the post-dam zones (shoreline and NHWZ) than in the OHWZ or desert scrub (Table 3). Among species, the common side-blotched lizard (*Uta stansburiana*), western whiptail (*Cnemidophorus tigris*) (Fig. 4a), desert spiny lizard (*Sceloporus magister*) (Fig. 4b), and ornate tree lizard (*Urosaurus ornatus*) show dramatic preference for the nearshore riparian (=NHWZ) and shoreline habitats. Interestingly, the densities of lizards found along the river corridor are higher than any other area in the southwest (Warren and Schwalbe 1988). This suggests that the riparian habitat created by Glen Canyon Dam is somehow unusual in its structure and/or productivity.

Table 3b. Lizard densities in habitats along the Colorado River in Grand Canyon, Arizona during June 1985. Values are mean number of individuals per hectare.

Habitat	Lizard Species					All Lizards
	Uta	Cnemidophorus	Sceloporus	Urosaurus	Crotaphytus	
Shoreline (<5m)						
Rocky Shore	94	17	53	37	1	202
Cobble Bar	69	10	14	33	0	126
Cliff Face	0	0	200	350	0	550
River Riparian (>5m)						
(NHWZ) Open Tamarisk	36	23	27	0	0	86
Arrowweed	39	78	7	0	0	123
Dense Tamarisk	0	41	30	0	0	71
(OHWZ) Terrace	22	9	14	0	0	45
Talus	9	0	10	0	0	19
Non-River						
Desertscrub	23	4	3	0	1	31
Grand Mean (All habitats)	43	13	20	14	0.4	90

Table 3. Lizard abundances along the Grand Canyon river corridor (Warren and Schwalbe 1988)

(a) (b)

Figure 4. The western whiptail (a) and the desert spiny lizard both occur in high numbers in the post-dam NHWZ and shoreline habitats.

There are several explanations for why lizard numbers may have increased following the closure of Glen Canyon Dam. First, lizards that were formally relegated to habitat above the high water line have been able to move downslope and extend their range with the stabilization of water levels and elimination of floods (Warren and Schwalbe 1988; Carothers and Brown 1991; Carothers et al. 1979). Second, the increase in riparian vegetation that followed the establishment of the dam may have had both a direct and indirect effect on lizards. The direct effect is that vegetation provides more structural heterogeneity and thereby creates more habitat diversity which can support more species and individuals. The indirect effect (which is probably of greater importance) is that the increase in riparian vegetation has led to an increase in insect numbers. As with amphibians, most lizards rely on insects for food, and therefore an increase in their food resources allows for an increase in population numbers (Carothers and Brown 1991).

The apparent increase in lizard numbers was an unforeseen side effect of the creation of Glen Canyon Dam. Now, with the fluctuating flows and experimental releases that are being put into effect, we can expect that lizard numbers may fluctuate as well. Rising waters during fluctuating flows have the potential to trap individuals on cobble and alluvial bars and drown them (Warren and Schwalbe 1988; US Dept. of Interior 2002). However, Warren and Schwalbe (1988) suggest that if ramping rates are kept below 3-4 feet per day, these mortalities should be minimal because most individuals would be able to escape before the water stranded them (US Dept. of Interior 2002). The derivation of this value is not specified in their paper, and a given flow level will cause varying feet per day rises depending on canyon morphology at a given reach. Winter high flows are also more likely to drown slow moving lizards. Another possible consequence of high flows is damage to annual reproduction. Warren and Schwalbe (1988) found that reproduction levels are highest in the shoreline and riparian zones. Because lizards build "nests" (bury eggs) in riparian areas that may be inundated during fluctuating flows, then high flows that occur during breeding and egg-laying season (April to July) are likely to destroy nests (US Dept. of Interior 2002). Therefore, if we wish to avoid mortality of lizards and their eggs, then dam management should avoid high flows during April to July and minimize ramping rates.

There are several species of snake along the river corridor, most of which are highly secretive. Little is known about the habitat dependence, abundance, and habits of the snakes of the Grand Canyon. One species that we know favors riparian habitat is the Grand Canyon rattlesnake (Reed and Douglas 2002) (Fig. 5). This rattlesnake is a subspecies unique to the Grand Canyon and adjoining tributary canyons, and shows a preference for the NHWZ (Miller et al. 1982; Carothers and Brown 1991). Other snake species probably utilize the riparian habitat mainly for foraging. Because both lizard and rodent (see next section) populations have probably increased since the dam was installed, and snakes use these animals as prey items, we can infer that many snake populations have likely increased as well (Carothers and Brown 1991).

Figure 5. The Grand Canyon rattlesnake prefers riparian habitat and inhabits the new riparian zones in the river corridor. (Source: John L. Broughton).

The main effects of experimental flows are likely negative. High flows, especially during winter months when snakes are hibernating, are likely to cause some mortalities due to drowning (US Dept. of the Interior 2002). Additionally, the possible reduction in riparian vegetation (due to scour) and direct mortality of lizards and small mammals may lead to a decrease in prey availability for snakes. This in turn could cause a decrease in snake populations via starvation or reduced reproduction. In general, snake numbers are likely to decline slightly following high flow events.

For both lizards and snakes, we must remember that the current population levels are likely to be elevated from pre-dam conditions, and therefore some mortality following high flows is probably acceptable. However, monitoring is an important tool for verifying that high flows are not overly damaging to reptile populations, and hence population monitoring of reptiles pre- and post-high flows should be implemented.

Mammals

The effect of Glen Canyon Dam on mammals seems to generally be positive or none (Table 4). However, since we do not have any data on abundances of mammals before the dam was built, this statement is again based on the natural history of Grand Canyon mammals combined with the known changes in the river corridor ecosystems. The ways in which mammals are affected by the dam varies by group, so I will discuss several groups individually: beaver and other aquatic mammals, small rodents, omnivorous scavengers, bats, carnivores, and large ungulates.

Species	**Pre-Dam Abundance**	**Post-Dam Abundance**	**Habitat Preference**	**Riparian or Aquatic Dependence**	**Effect of Glen Canyon Dam**
Yuma myotis *Myotis yumamensis*	Common	Common	Desert, riparian	High	Unknown
California myotis *Myotis californicus*	Abundant	Abundant	Desert, riparian	High	Unknown
Silver-haired bat *Lasionycteris noctivagans*	Rare	Rare	Desert, riparian	Low	Unknown
Western pipistrelle *Pipistrellus hesperus*	Abundant	Abundant	Desert, riparian, conifer	Low	Unknown
Big brown bat *Eptesicus fuscus*	Uncommon	Uncommon	Desert, riparian	Low	Unknown
Townsend's big-eared bat *Plecotus townsendii*	Rare	Rare	Desert, riparian	Low	Unknown
Pallid bat *Antrozous pallidus*	Common	Common	Desert, riparian	Low	Unknown
Brazilian free-tailed bat *Tadarida brasiliensis*	Uncommon	Uncommon	Desert, riparian	Low	Unknown
Beaver *Castor canadensis*	Common	Common/ Abundant	Streams and mainstem sand banks	Very High	Positive
Rock squirrel *Spermophilus variegatus*	Common	Common	Desert, riparian	Low	Positive?
Harris' antelope squirrel *Ammospremophilus harrisii*	?	Rare	Desert, riparian		Unknown
White-tailed antelope squirrel *Ammorspermophilus leucurus*	Uncommon	Uncommon	Desert, riparian	Low	Unknown

Merriam's kangaroo rat *Dipodomys merriami*	Uncommon	Uncommon	Desert, riparian	Low	Unknown
Cliff chipmunk *Eutamias dorsalis*	Uncommon	Uncommon	Cliffs, Desert, riparian	Low	Unknown
Long-tailed pocket mouse *Perognathus formosus*	Uncommon	Uncommon	Desert, riparian	Low	Unknown
Rock pocket mouse *Perognathus intermedius*	Common	Common	Desert, riparian	Low	Unknown
Western harvest mouse *Reithrodontomys megalotis*	Uncommon	Uncommon	Desert, riparian	Medium	Unknown
Canyon mouse *Peromyscus crinitus*	Abundant	Abundant	Desert, riparian	Medium	Positive?
Cactus mouse *Peromyscus eremicus*	Abundant	Abundant	Desert, riparian	Medium	Positive?
Deer mouse *Peromyscus maniculatus*	Uncommon along corridor	Common	Riparian	High	Positive
Brush mouse *Peromyscus boylii*	Uncommon	Uncommon	Desert, riparian	Medium	Positive
Pinyon mouse *Peromyscus truei*	Rare	Rare	Desert, riparian	Low	Positive
White-throated woodrat *Neotoma albigula*	Abundant	Abundant	Desert	Low	Probably none
Desert woodrat *Neotoma lepida*	Abundant	Abundant	Desert	Low	Probably none
Muskrat *Ondatra zibethicus*	Rare	Rare	Aquatic, riparian	Very High	Potentially positive, but none
River otter *Lontra canadensis*	Uncommon	Rare or extirpated	Aquatic and riparian of mainstem and tributaries	Very High	Potentially positive, but none
Coyote *Canis latrans*	Uncommon	Uncommon	Desert, riparian	Medium	Unknown
Gray fox *Urocyon cinereoargenteus*	Uncommon	Uncommon	Desert, riparian	Medium	Unknown
Ringtail *Bassariscus astutus*	Common	Common	Desert, riparian	Medium	Positive (indirect)
Racoon *Procyon lotor*	Rare	Rare	Riparian	High	Unknown
Western spotted skunk *Spilogale gracilis*	Common	Common	Desert, riparian	Medium	Positive (indirect)
Mountain lion *Puma concolor*	Rare	Rare	Desert, riparian	Low	Unknown
Bobcat *Lynx rufus*	Rare	Rare	Desert, riparian	Low	Unknown
Mule deer *Odocoileus hemionus*	Common	Common	Desert, riparian	Medium	Unknown

Bighorn sheep *Ovis canadensis*	Common	Common	Desert, riparian	Medium	Positive?
Feral burro *equus asinus*	Common	Absent (mostly)	Desert, riparian	Medium	None—removed

Table 4. Mammals. Information from Hoffmeister (1971), Ruffner et al. (1978), and Carothers and Brown (1991). Current species names from Whitaker (1998).

Beaver (Fig. 6) are common throughout the canyon, despite the apparent lack of suitable habitat. They inhabit both tributary streams, where they build dams, and the mainstem of the Colorado River, where they build bank dens (Hoffmeister 1986; US Dept of the Interior 2002). Beaver rely on cottonwoods (*Populus* sp.), willows, and the exotic tamarisk for food in the Grand Canyon (Hoffmeister 1971). Due to the increase in willow and tamarisk since the closure of Glen Canyon Dam, beaver abundance has likely increased also. Additionally, the flattening of the river's hydrograph has led to a more predictable flow regime. Since beavers make bank dens that have dry chambers above the high water line, this stabilization of the flow regime has allowed higher success of bank dens (Carothers and Brown 1991). Beavers reproduce and keep their young in these bank dens, so the lack of floods prevents their young from drowning and probably allows them to build dens lower down in the banks.

Figure 6. Beaver have benefited from an increase in food resources and space for bank dens. (Source: www.scotsbeaver.com)

Experimental flows may be hazardous to beavers. Extended low flows could decrease the availability of their staple foods, while high flows may drown young (or even adults) in their bank dens (US Dept of the Interior 2002). These two possible effects should be considered in determining how flows are designed and implemented.

There are two other aquatic vertebrates that may exist in the Grand Canyon. Both river otter (Fig. 7) and muskrat have been sighted infrequently along the river corridor, but no recent sightings exist. Presumably, the habitat changes in the Grand Canyon since the closure of Glen Canyon Dam should favor river otter and muskrat, which both thrive along vegetated shorelines (Hoffmeister 1986; Carothers and Brown 1991). Fish, a common food staple of river otters, are also prevalent in the Colorado River and therefore food resources are available. However, neither species has become established, possibly due to a simple lack of migrating individuals. A proposal has been put forth to "reintroduce" river otters, but the idea is fraught with controversy. If either river otter or muskrat were to become established, controlled floods and fluctuating flows would likely cause a decrease in suitable habitat and a subsequent decrease in population size. However, these species seem to have always been marginal in the Grand Canyon, and hence should not be focused on for management considerations.

Figure 7. River otters are now rare or extirpated from the canyon, although current changes in riparian vegetation should favor their existence. (Source: www.enature.com/fieldguide).

The overall effect of the dam on small rodents seems to have been positive (Carothers and Brown 1991). There is only one small rodent in the river corridor that absolutely requires riparian habitat—the deer mouse (*Peromyscus maniculatus*) (Fig 8a). However, there are many rodent species that use the riparian zone (US Dept. of the Interior 1994). In fact, all eight mice species from the river corridor have successfully colonized the NHWZ (Carothers and Brown 1991). Small rodents that utilize riparian habitat have benefited from an increase in riparian vegetation, which provides both food and protective cover to prevent predation. The deer mouse in particular has experienced a large increase in abundance along the mainstem of the river (Carothers and Brown 1991). Prior to the dam, deer mice occurred only along the riparian zones of the tributaries, but now they are widespread along the corridor where dense riparian vegetation is available (Carothers and Brown 1991). The pinyon and brush mouse, which were absent and rare (respectively) on the corridor before 1963, also increased in abundance after the dam was installed (Carothers and Brown 1991).

(a) (b)

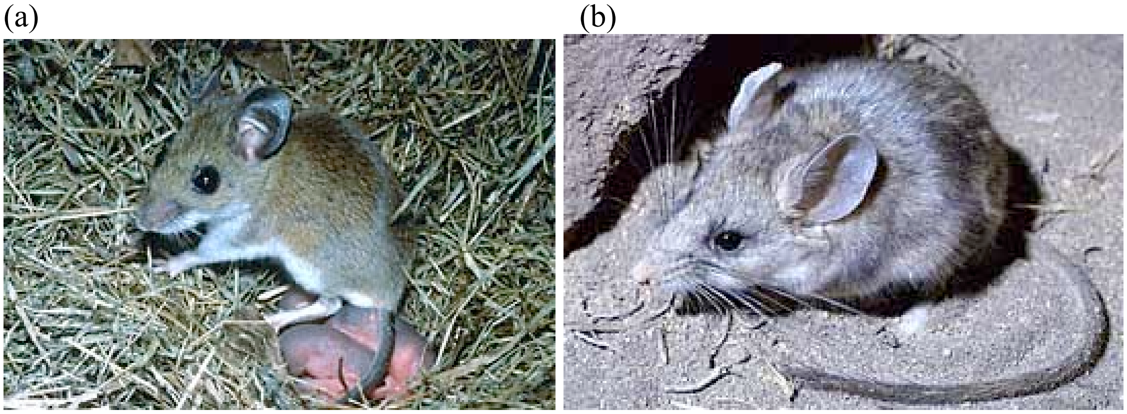


Figure 8. The deer mouse (a) and pinyon mouse (b) have both increased in numbers since the dam was installed. (Source: John McDonald www.enature.com/fieldguide and Ronn Altig www.enature.com/fieldguide).

Campers and river runners also serve as a new food source for small mammals along the Colorado River. This extra food has probably led to an increase in small mammal populations, including species such as the rock squirrel (*Spermophilus variegatus*) (Carothers et al. 1979). However, food provided by campers may serve as "junk food" to these small mammals and therefore does not promote healthy populations. Rock squirrels in poor health are common sights along the river (Carothers et al. 1979).

The effects of fluctuating flows and controlled floods on small rodents will probably be minimal. Some individuals may be lost to drowning, especially young litters, but most should be able to move upslope. Since the deer mouse has 2-4 litters each year, one of its litters may be drowned if flows occur anytime between February and November (US Dept of the Interior 2002). However, the other litters will still allow for successful recruitment at different times during the year. A decrease in riparian vegetation due to current management flows may also decrease habitat and food availability for small mammals, and thereby decrease population numbers. But, since small mammals have rapid reproduction and are currently abundant in the corridor, recovery from high flow events should be rapid.

Omnivorous scavengers within the canyon, namely ringtail (*Bassariscus astutus*) (Fig. 9a) and western spotted skunk (*Spilogale gracilis*) (Fig. 9b), have likely increased in numbers due to the dam's presence. This may be due directly to an increase in available riparian habitat following flow stabilization. However, a more important factor is probably the increase in campers and river runners in the canyon since the dam was closed. Visitation to the river corridor has increased dramatically in the past few decades (Carothers et al. 1979), and with visitors comes a large supply of food. Ringtails and western spotted skunks are known to steal food from campers and have likely benefited from this extra food source (Carothers et al. 1979; Carothers and Brown 1991). Current dam operations will probably have little effect on these two species because river runners and campers will continue to be present in the corridor, despite experimental flows.

(a) (b)

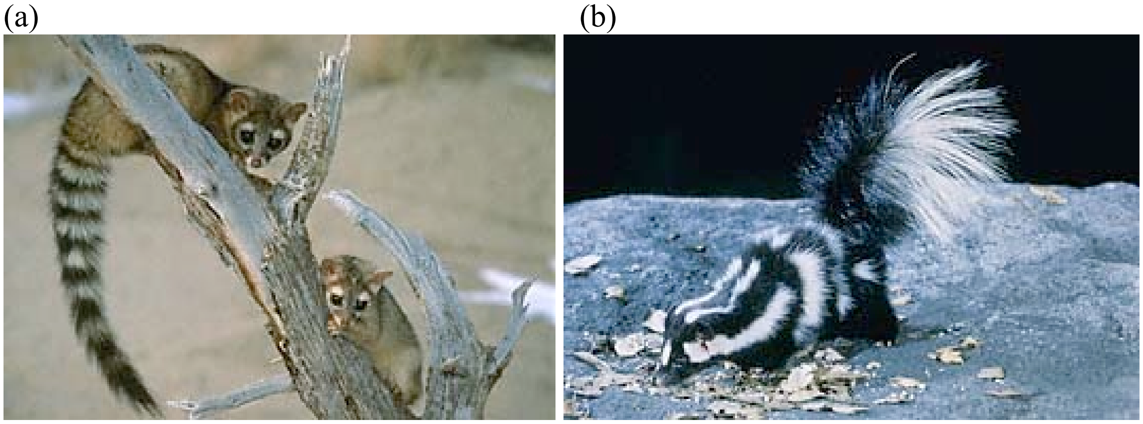


Figure 9. Ringtails (a) and western spotted skunks (b) both steal food from campers and river runners, and may have benefited from this new food source. (Source: www.enature.com/fieldguide).

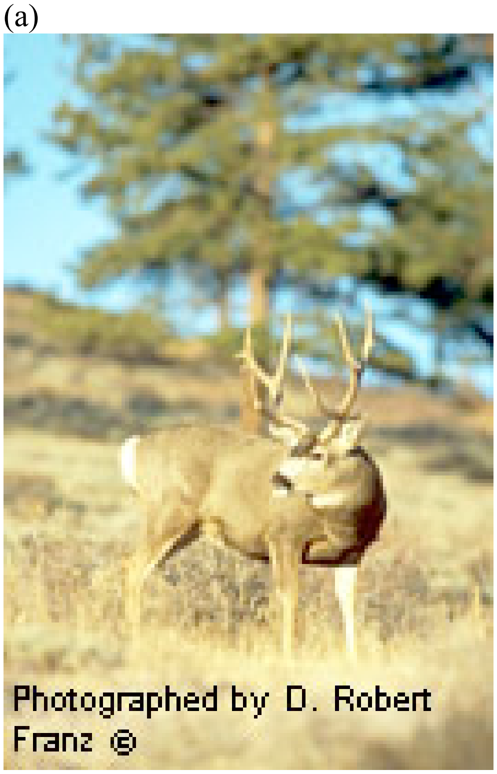
Effects of the dam on bats (Fig. 10) are unclear. Carothers and Brown (1991) suggest that bats have increased since the dam was installed because of the increase in insects (their food). However, Webb et al. (2003) found that old river runners thought that bats had declined in number since the pre-dam days. Since bats are known to abandon roost sites that have been disturbed by people (O'Shea and Vaughan 1999), it is possible that the increase in recreational use of the canyon may be pushing bat populations out of the canyon. Together, these two effects may be canceling each other out, or one may be overwhelming the other. Bat populations fluctuate widely throughout the year and between years, so population monitoring should be started to determine what the abundances are of different species. The effects of experimental releases are hard to predict since we do not understand how post-dam bat populations compare to pre-dam populations.

Figure 10. The pallid bat is one of many bat species in the Grand Canyon. Effects of Glen Canyon Dam on bat populations are not well understood. (Source: www.enature.com/fieldguide).

Carnivores are likely affected by the dam in an indirect way. All of the carnivores of the Grand Canyon river corridor are uncommon or rare (except for the omnivorous scavengers discussed above), probably because it is difficult to move around the canyon and food resources are limited. However, carnivore populations may still be affected by the change in flow regime via fluctuations in prey populations (especially small mammals). These effects are likely to be minimal because carnivores generally have large ranges and can extract prey from both riparian and desert communities.

Large ungulates of the Grand Canyon corridor include mule deer (*Odocoileus hemionus*) (Fig. 11a) and bighorn sheep (*Ovis canadensis*) (Fig. 11b). Both were common along the Colorado River before the dam, and both remain common today. Bighorn sheep use the river as a summer water source (Hoffmeister 1971) and may also forage on riparian vegetation. Some anecdotal evidence suggests that bighorn sheep may have increased in abundance since the dam was built (Webb et al. 2003), but this evidence is based on observations only. Regardless of how the Glen Canyon Dam's presence initially affected these ungulates, they seem to be thriving within the new river regime. Fluctuating flows and floods are not likely to affect mule deer or bighorn sheep because they are highly mobile and use a variety of habitats within the canyon.

(a)



(b)

Figure 11. Mule deer (a) and bighorn sheep (b) were both common before the dam, and remain common now. The dam may have allowed for slight increases in the populations of these ungulates. (Source: D. Robert Franz and www.azdfg.gov).

In general, the presence of Glen Canyon Dam has led to an increase or no change in mammal populations. The current Adaptive Management practices may lead to decreases in mammal populations that have increased since dam closure, but will probably have a significant effect on only a few species, such as beavers and small rodents.

CONCLUSION

The effects of Glen Canyon Dam on the wildlife of the Grand Canyon river corridor will never be entirely clear due to a lack of pre-dam abundance information. However, using inferences based on current abundances, the change in riparian communities, and species' natural history, it seems that most amphibian, reptile, and mammal populations have either increased or remained the same (Table 5). Fluctuating flows and floods may diminish this effect by causing a decrease in some of the riparian-dependent species, although management planning can be used to minimize this effect. Also, many of these riparian species are quite resilient to flooding. For example, Warren and Schwalbe (1988) found that lizard populations recovered fully one year after the "natural" 1983 flood. This means that the diminishing effects of experimental flows are likely to be temporary. Finally, I want to stress the importance of remembering that current high numbers of lizards, small rodents, ringtail, spotted skunks, toads, beavers, and others are likely attributable to direct and indirect effects of the dam itself. Therefore, I believe that some losses of individuals are acceptable if they are due to Adaptive Management practices that aim to restore other aspects of the Colorado River. Most importantly, I think that full monitoring of riparian species within the canyon should be undertaken in order to ensure that there are no unforeseen effects of fluctuating flows on the wildlife of the river corridor. The wildlife within the Grand Canyon are a draw for many tourists, and help gain support for preservation of less visible species such as the humpback chub. To guarantee future support of wildlife projects in the Grand Canyon, it is important to maintain healthy populations of terrestrial wildlife.

Taxon	No. species	# Positive	# Negative	#No effect	#Unknown
Amphibia	4	3	0	1	0
Reptiles	23	10	0	3	10
Mammals	36	10	0	5	21
Birds	373	49	5	306	13
Total (#/%)	436	72/16.5%	5/1.2%	315/72.2%	44/10.1%

Table 5. Summary of effects of Glen Canyon Dam on terrestrial wildlife of Grand Canyon river corridor. #positive includes "positive" and "positive?". Bird data from Schell (2005, this volume) and includes all bird species within the Grand Canyon National Park—not just river corridor species. The "#positive" category for birds includes "positive" and "may be increasing". The "no effect" category for birds is all species that Schell did not analyze.

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