

# The western pond turtle (*Clemmys marmorata*) in the Mojave River, California, USA: highly adapted survivor or tenuous relict?

Jeff Lovich<sup>1\*</sup> and Kathie Meyer<sup>2</sup>

<sup>1</sup> United States Geological Survey, Western Ecological Research Center, 7801 Folsom Boulevard, Suite 101, Sacramento, CA 95826, U.S.A.

<sup>2</sup> United States Geological Survey, Western Ecological Research Center, San Diego Field Station, 5745 Kearny Villa Road, Suite M, San Diego, CA 92123, U.S.A.

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## Abstract

Aspects of the ecology of populations of the western pond turtle *Clemmys marmorata* were investigated in the Mojave River of the central Mojave Desert, California, U.S.A. One population occupied man-made ponds and the other occurred in natural ponds in the flood plain of the Mojave River. Both habitats are severely degraded as a result of ground water depletion from human activities along the river and one is infested with the exotic shrub saltcedar *Tamarix ramosissima*. Mean female carapace length (CL) was significantly greater (14.4 cm) than that of males (13.7 cm). Live juveniles were not detected during the period of study. Shelled eggs were visible in X-radiographs from 26 May to 14 July. Mean clutch size was 4.46 and ranged from 3 to 6 eggs. Clutch size did not vary between 1998 and 1999 but was significantly correlated with CL for both years combined, increasing at the rate of 0.548 eggs/cm CL. Gravid female CL ranged from 13.3–16.0 cm. Some females nested in both years. Mean X-ray egg width (21.8 mm) was not significantly correlated with CL or clutch size. X-ray egg width differed more among clutches than within, whether including CL as a co-variate or not. Nesting migrations occurred from 6 June to 8 July with minimum round trip distances ranging from 17.5–585 m with a mean of 195 m. Mean estimated time of departure as measured at the drift fence was 18:13. Most females returned to the ponds in the early morning. Nesting migrations required females to be out of the water for estimated periods of 0.83 to 86 h. The destination of nesting females was typically fluvial sand bars in the channel of the dry riverbed. Overall, the ecology of *C. marmorata* in the Mojave River is very similar to that reported for populations in less severe habitats along the west coast of the United States. Notable exceptions include long nesting migrations to sandbars in the dry river channel, a possible result of human modifications to the environment, and an apparent lack of terrestrial overwintering behaviour in Mojave River populations. The general similarity of desert and coastal populations is possibly a reflection of their recent geographic separation. Overall, populations in the Mojave River exhibit few obvious adaptations to living in the desert and are considered to be tenuous relicts of the Pleistocene. The small size and tenuous status of these populations suggests that immediate conservation action is needed, including establishment of satellite populations as a hedge against extirpation.

**Key words:** *Clemmys marmorata*, ecology, adaptation, Mojave Desert, California

## INTRODUCTION

Adaptation of organisms to their environment is the process by which populations acquire traits that tend to enhance survivorship, mating success, and fertility (Templeton, 1982). As such, adaptation is both a process and a product, the product being the specific

genetically determined traits that make an organism more likely to survive and produce viable offspring (Cole, 1954). In contrast, acclimation is the non-genetic process whereby phenotypes are determined by the environment (McNaughton & Wolf, 1979). For example, organisms can be adapted to living in a wide range of environmental conditions, but local conditions may produce populations with different sizes, colours, behaviours or other attributes within the fixed range of adaptation. Understanding the roles of adaptation and

\*All correspondence to: Jeff Lovich.  
E-mail: jeffrey\_lovich@usgs.gov

phenotypic plasticity exhibited under acclimation is important to elucidating the significance of differences among populations of the same species inhabiting different environments.

The western pond turtle *Clemmys marmorata* is a wide-ranging species that formerly occurred from extreme western Washington, U.S.A., and possibly British Columbia, Canada, to northern Baja California, Mexico, mostly to the west of the Cascade-Sierra crest (Ernst, Lovich & Barbour, 1994). Disjunct populations exist, or existed, in the Truckee, Humboldt, and Carson Rivers in Nevada, Puget Sound, and the Columbia Gorge, U.S.A. Another isolated, but extant, population is found in the interior-draining Mojave River of southern California, U.S.A., well into the center of the Mojave Desert. The western pond turtle is the only native aquatic turtle in the Mojave Desert ecosystem of California (Ernst *et al.*, 1994), a fact that is not surprising in light of the extreme aridity of the region. Populations of *C. marmorata* in the Mojave Desert have the additional distinction of being one of the few emydid turtles to occupy wetlands in true deserts, with the exceptions of the Mediterranean terrapin *Mauremys leprosa* in Algeria and Morocco (Loveridge & Williams, 1957), and the aquatic box turtle *Terrapene coahuila* in the northern Chihuahuan Desert of Mexico (Brown, 1974). In California, where modern populations are small and dwindling (Brattstrom, 1988; Brattstrom & Messer, 1988; Buskirk, 1990), *C. marmorata* is protected by the California Department of Fish and Game as a 'species of special concern' (Jennings & Hayes, 1994).

The wide latitudinal distribution of *C. marmorata* and the isolated nature of populations like those in the Mojave River provide an opportunity to assess the roles of adaptation and acclimation in this species. In this paper, we examine aspects of the ecology of two populations in the Mojave River and compare and contrast those data with published literature for populations from less arid portions of the range in an effort to elucidate the adaptations or acclimations that have allowed a semi-aquatic turtle to persist in the Mojave Desert. Knowledge of such factors is especially relevant to efforts aimed at conserving populations of this sensitive species in degraded habitats. Our data are tested against the null hypothesis that these populations are neither highly adapted nor acclimated to the harsh conditions imposed by the Mojave Desert and thus will exhibit ecological traits and behaviours that are similar to coastal and interior valley populations.

## MATERIALS AND METHODS

### Site descriptions

We conducted research from May, 1998 to October, 1999 at the Afton Canyon Area of Critical Environmental Concern (ACEC), administered by the Bureau of Land Management (BLM), and the Camp Cady Wildlife Area, administered by the California Depart-

ment of Fish and Game. Both are located in the central Mojave Desert of San Bernardino County, California, U.S.A. Wildlife is protected at both locations, although certain bird species are hunted at Camp Cady during part of the year. The climate in the area is characterized by hot dry summers and cool winters with frontal precipitation, most of which falls as rain. Rainfall at nearby Barstow, California averaged 112 mm annually from 1897–1996. The average annual min. temperature from 1913–1996 was 8.9 °C and ranged from 6.4–11.6 °C. The average annual maximum temperature from 1913–1995 was 26.9 °C and ranged from 24.8–28.9 °C. However, daily temperatures routinely fall to about 0 °C in the winter and exceed 43 °C in the summer (Hereford & Longpré, 1999).

The Mojave River is about 200 km in length from its headwaters in the San Bernardino Mountains to its terminus in the Cronese Dry Lakes. With no outlet to the ocean, the river lies within the hydrographic boundary of the Great Basin (Grayson, 1993). Although it formerly flowed well into the desert prior to excessive water use by humans in the 20th century, the river is typically dry along most of its length, except during years with extraordinary precipitation. Vegetation along much of the desert course of the river was long dominated by native riparian species including cottonwoods *Populus fremontii*, willows (*Salix gooddingii*, *S. exigua*, *S. laevigata*, and *S. lasiolepis*), and mesquite (*Prosopis glandulosa*, and *P. pubescens*). However, during the 20th century, much of the riparian zone was replaced with the exotic pest plant saltcedar *Tamarix ramosissima*, also known as tamarisk (Lovich, Egan & de Gouvenain, 1994; Lovich & de Gouvenain, 1998). Detailed descriptions of the vegetation at Camp Cady and along the Mojave River are given by Lines & Bilhorn (1996).

Aquatic habitat for *C. marmorata* at Camp Cady is currently restricted to 3 artificial ponds, less than 2 m in depth, and maintained by inputs of ground water from on-site wells. The ponds have a combined surface area of about 0.5 ha, and are perched just beyond the edge of the river terrace and flood plain. Only 2 ponds are typically occupied by *C. marmorata*, the third being a small pond maintained as a source of water for fire suppression. During the course of our study, the river bed was dry at Camp Cady. However, in wet years, especially those characterized by El Niño/Southern Oscillation events, the river here is an ephemeral stream. A healthy cottonwood gallery forest is located within about 50 m of the ponds.

At Afton Canyon, about 30 river km downstream from Camp Cady, *C. marmorata* occupies permanent natural pools of water (max. depth about 1.5 m) in the flood plain of the Mojave River. Total surface area of these ponds is less than 0.25 ha. The habitat is dominated by saltcedar, cattails *Typha domingensis*, sedges (*Scirpus pungens* and *S. maritimus*), reeds *Phragmites australis*, and salt grass *Distichlis spicata*. This is the last permanent water, and last population of *C. marmorata*, on the Mojave River before its terminus at the Cronese Dry Lakes.

Populations at the 2 study sites are completely isolated in most years as the intervening river bed is dry except during years characterized by exceptional precipitation, especially El Niño/Southern Oscillation events. Even then, movement between sites is expected to be downstream only, with individuals from Camp Cady potentially being displaced to Afton Canyon during floods.

## Methods

Thirty-seven individual *C. marmorata* were captured in traps or observed a total of 193 times (including recaptures, radio fixes, and drift fence interceptions) from May 1998 to November 1999. Most turtles were captured in aquatic traps baited with canned sardines (Gibbons, 1990). Data collected from each turtle included straight-line carapace length (CL) and plastron length (PL) to the nearest mm. Carapace length was recorded along the midline from the anterior of the cervical scute to the posterior margin of the carapace. We measured PL along the midline of the plastron from the anterior of the gular scute midline to the anal notch. Weight was recorded to the nearest g upon each physical capture. We determined the sex of turtles using diagnostic characters given in Ernst *et al.* (1994).

Females were checked for shelled eggs, whenever possible, by X-radiography or hand palpation. When females were X-rayed, we followed the technique described in Hinton *et al.* (1997) using rare-earth cassettes (60 kV, 0.08 s, 73.7cm focal distance) to minimize exposure to the turtles. X-radiograph egg widths (XREW) were measured from X-radiographs using dial calipers.

In an effort to intercept nesting females, drift fences and pitfall traps (19 litre plastic buckets) were placed around the perimeter (about 3 m from the waterline) of the ponds at Camp Cady in 1999 following the method of Gibbons & Semlitsch (1981). Pond 3 was completely encircled and pond 2 was fenced on its eastern half, both from 12 May to 12 July. During that time period we walked the perimeter of the fence approx. once every 60 min from 06:30 to 19:30 to look for turtles. Fence gates were opened and lids were placed on the pitfall traps for several days when we were unavailable, allowing some females to leave the ponds undetected.

Females captured during the nesting season along the inside of the fence, or in buckets, were assumed to be on nesting forays. Upon capture, they were temporarily fitted with a small radio transmitter, weighing 1.7 g, and then released immediately outside of the fence. Most females were palpated by hand for the presence of shelled eggs and X-rayed as equipment was available. We tracked and observed (at irregular intervals between 07:00 and 20:00) radio-tagged female turtles that left the ponds until they returned to the drift fence. At that time, the radio was removed and they were placed back in the pond. A Precision Lightweight Global Positioning unit was used to determine coordinates at various point

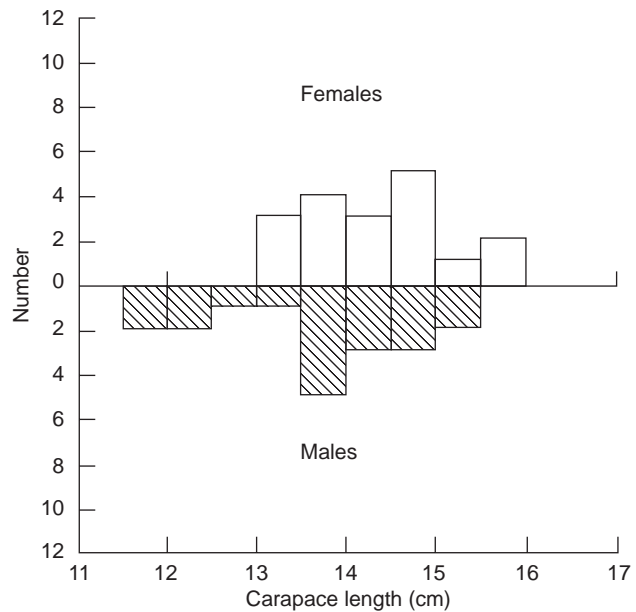


Fig. 1. Histogram showing carapace length distribution of *Clemmys marmorata* from the Mojave River, California.

locations along the excursion path. Site fixes were accurate to within about 5 m. Turtles of both sexes were fitted with radio-transmitters at Afton Canyon to assess movements and habitat use intermittently throughout the year (site fixes were taken during January, April, June–September, and November).

Analysis of the circular scale variable time was made using Oriana<sup>©</sup> software for circular statistics. All other statistical analyses used SYSTAT (Wilkinson, 1988). We estimated population sizes using Program Capture (White *et al.*, 1982). Means are reported  $\pm 1$  standard deviation (SD).

## RESULTS

### Demographics

Female CL was significantly greater than male CL ( $t = 2.03$ ,  $P = 0.05$ , d.f. = 35). Mean CL of males was  $13.7 \pm 1.17$  cm (range 11.7–15.5 cm,  $n = 19$ ). Mean CL of females was  $14.4 \pm 0.811$  cm (range 13.2–16.0 cm,  $n = 18$ ) (Fig. 1). Mean female weight was  $523 \pm 80.1$  g (range 400–750 g,  $n = 18$ ). Mean male weight was  $406 \pm 78.9$  g, (range 265–533 g,  $n = 18$ ). The overall adult sex ratio was 19 males: 18 females. The sex ratio at Afton Canyon was 7 males: 7 females, while at Camp Cady it was 12 males: 11 females. None of the sex ratios were significantly different from unity. No turtles smaller than 11.7 cm CL were trapped during our study.

At Camp Cady in 1998 we captured 21 turtles 38 times during 10 aquatic trapping occasions. Program Capture selected a model, Chao's  $m(th)$  – incorporating heterogeneity of both individuals and time – to estimate

a population size of 25 (SE = 3.28) with a 95% confidence interval (CI) of 23–37. At Afton Canyon in 1998 we captured 14 turtles 30 times during seven aquatic trapping occasions. Program Capture recommended the same model with an estimated population size of 16 (SE = 1.87) and a 95% CI = 15–23.

Using population estimates and confidence intervals from Program Capture, we estimated standing crop biomass assuming a mean mass per adult turtle of 410 g. If there were 25 turtles at Camp Cady, then the biomass estimate is 20.49 kg/ha (95% CI = 18.85–30.33 kg/ha). For an estimated 16 turtles at Afton Canyon, the biomass estimate was 26.23 kg/ha (95% CI = 24.59–37.71 kg/ha). The population estimates suggest densities of 50 turtles/ha (95% CI = 46–74 turtles/ha) and 62 turtles/ha (95% CI = 60–92 turtles/ha) at Camp Cady and Afton Canyon, respectively.

## Reproduction

Shelled eggs were visible in X-radiographs from 26 May to 14 July. Mean clutch size from 12 (including two from Afton Canyon and 10 from Camp Cady) from 10 X-radiographed females was  $4.58 \pm 0.90$  eggs (range 4–6 eggs). Mean clutch size in 1998 was  $4.8 \pm 1.095$  eggs ( $n = 5$ ) and was not significantly different from the mean clutch size of  $4.4 \pm 0.787$  eggs in 1999 ( $n = 7$ ), as shown by Student's *t*-test ( $t = 0.687$ , d.f. = 10,  $P = 0.51$ ). X-radiographed clutch size was significantly correlated with CL as shown by linear regression ( $r^2 = 0.33$ ,  $P = 0.05$ , d.f. = 1, 10), increasing at the rate of 0.548 eggs per cm increase in CL. Mean CL of females, verified as gravid using X-radiography, was  $14.4 \pm 0.98$  cm (range 13.3–16.0 cm,  $n = 10$ ).

Mean XREW was  $21.8 \pm 0.82$  mm (range 19.0–23.0 mm,  $n = 55$ ) and XREW was not significantly correlated with CL ( $r^2 = 0.01$ ,  $P = 0.51$ , d.f. = 1, 53) or clutch size ( $r^2 = 0.01$ ,  $P = 0.43$ , d.f. = 1, 53). XREW differed more among clutches than within whether using CL as a co-variate (ANOVA,  $F = 4.34$ ,  $P = 0.001$ , d.f. = 8 [individual], 1 [CL], 45 [error]), or not (ANOVA,  $F = 3.940$ ,  $P = 0.001$ , d.f. = 9, 45).

A single nest containing three eggs was located at Camp Cady on 11 June, 1998 as it was being excavated by the female just inside of the drift fence. When uncovered for examination on 19 November, 1999 all the embryos were dead, reduced to skeletons. The embryos were at full term development, completely filling the largely intact eggs. Egg length of the most complete egg was 37.04 mm. Carapace lengths of the embryos were 25.6, 25.7, and 27.9 mm (mean =  $26.4 \pm 1.3$  mm). The nest was flask-shaped and approximately 7 cm in depth. Ants were observed in the nest chamber.

X-radiography and hand palpation suggest that shelled eggs may be carried for up to 3 weeks before being oviposited. Two females produced clutches in both years.

**Table 1.** Data for female *Clemmys marmorata* making known and putative nesting migrations at Camp Cady, Mojave River, San Bernardino County, California. Abbreviations: ID (CL), individual identification code (carapace length); ETD, estimated time of departure from pond; ETA, estimated time of arrival at pond; Distance, total distance travelled in nesting migration

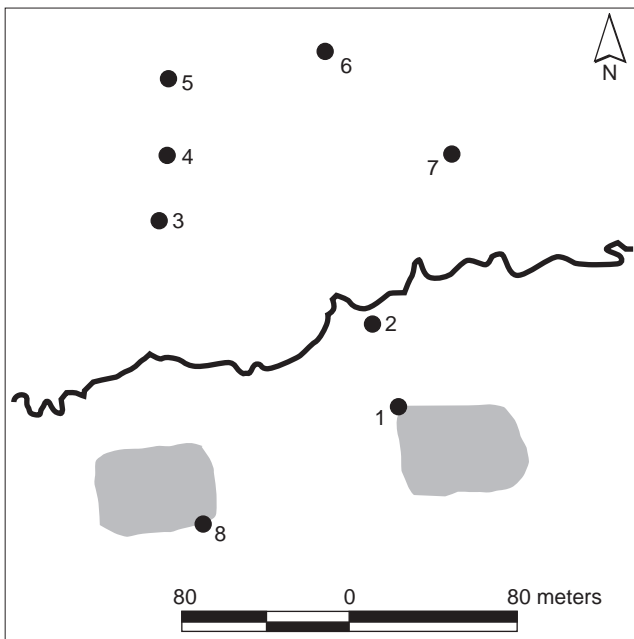
| ID(CL)      | Date       | ETD   | ETA   | Distance (m) | Hours on land |
|-------------|------------|-------|-------|--------------|---------------|
| AJN (14.5)  | June 6–7   | 18:30 | 08:00 | 24           | 13.50         |
|             | June 8–9   | 17:20 | 09:15 | 303          | 15.83         |
| ABHW (13.7) | June 7–8   | 07:05 | 11:30 | 379          | 28.58         |
| AKN (13.5)  | June 7–9   | 17:00 | 09:45 | 585          | 40.75         |
| AKM (16.0)  | June 11–12 | 17:00 | 07:45 | 212          | 14.75         |
|             | July 7–8   | 19:30 | 06:30 | 17.5         | 11.0          |
| AHV (15.7)  | June 11–12 | 19:15 | 06:30 | 25           | 10.75         |
|             | June 12–16 | 19:30 | 09:30 | 390          | 86.0          |
|             | July 7     | 17:15 | 20:00 | 74.9         | 2.75          |
| AJO (14.8)  | June 20–21 | 19:20 | 07:20 | 50           | 12.0          |
|             | June 23–24 | 18:30 | 19:50 | 242          | 25.33         |
| CJO (13.6)  | July 1     | 19:00 | 19:50 | 43           | 0.83          |
| Unknown     | June 11    | 17:20 | –     | –            | –             |

## Nesting migrations

Eight female *C. marmorata* made 13 known and putative nesting migrations between 6 June and 8 July. The vast majority of nesting migrations were oriented toward the dry channel of the Mojave River. Mean minimum round trip distance was  $195 \text{ m} \pm 187 \text{ m}$  (range 17.5–585 m,  $n = 12$ ).

Most females were captured at the drift fence leaving ponds in the evening (Table 1). The mean vector of estimated time of departure was 18:13 (95% CI = 16:44–19:41,  $n = 13$ ) and was statistically different from circular uniformity as shown by Rayleigh's test ( $P < 0.01$ ). In contrast, most females returned to the pond in the early morning. The mean vector of estimated time of arrival was 08:44 (95% CI = 05:08–12:20,  $n = 12$ ), but was not statistically different from circular uniformity as shown by Rayleigh's test ( $P = 0.09$ ), suggesting that the associated 95% CI estimate may be unreliable.

A typical nesting migration (Fig. 2) involved a series of movements punctuated by periods of inactivity under dense cover, including honey mesquite *Prosopis glandulosa* thickets, catclaw *Acacia greggii*, and leaf litter in dense groves of Fremont cottonwood trees *Populus fremontii*. One female sheltered in a barn near Pond 2 for a minimum of 10 h. At least one female returned to the pond without laying eggs, and three females returned to the pond only to leave again in a day or two. Nesting migrations required females to be out of water for estimated periods of from 0.83–86 h. The only confirmed nest was oviposited inside the drift fence under a quailbrush *Atriplex lentiformis* canopy on 11 June, less than 5 m from the water's edge. Because of the proximity to the drift fence, this female may have been prevented from going farther from the pond. The soil in this area had a high clay content.



**Fig. 2.** Map showing the locations occupied for a female *Clemmys marmorata* on a putative nesting excursion at the Camp Cady Wildlife Area. The jagged line represents the edge of riparian vegetation along the Mojave River and numbered solid circles represent sequential locations occupied by the turtle. Locations 3–7 are all located in the floodplain of the river. See individual identification code ‘AKN’ in Table 1 for details on the nesting excursion.

### Other movements

Of seven turtles (three females and four males) radio-tracked at Afton Canyon in 1998 and 1999, none were ever noted to leave the ponds. With the general exception of movements by Camp Cady females to find nest sites, the overall perception was one of wetland site-fidelity and dependence upon the aquatic environment during all seasons. Known occupied habitats at Afton Canyon included small, open-water ponds and shallow, interconnecting sloughs densely vegetated with *T. domingensis*. At Camp Cady, movements between Ponds 2 and 3 were recorded for one male and two females, a one-way distance of approx. 87 m.

### DISCUSSION

The ecology and behaviour of the *C. marmorata* populations along the Mojave River appear to be very similar to, and generally within the range of, that reported for other populations (Table 2). Maximum body size of Mojave River turtles is smaller than that reported for other populations. However, Holland (1994) observed that *C. marmorata* in southern California rarely exceed 16.0 cm, our maximum size. Population densities and standing crop biomass of Mojave River populations of

*C. marmorata* are low in comparison with other populations. Data reviewed in Holland (1994) suggest that densities may exceed 1000 turtles/ha in some stream habitats, while small ponds in Oregon may achieve densities of over 500 turtles/ha. However, these densities represent extremes and more typical reported densities range from 23–214 turtles/ha (Ernst *et al.*, 1994; Holland, 1994).

The absence of live juvenile turtles in our sample has two possible explanations. First, juvenile turtles often occupy different habitats than adults, eat different foods, and exhibit different behaviours. As such, juveniles tend to be notoriously under-represented in most turtle studies. Second, it is also possible that the absence of juveniles reflects a lack of recruitment in the populations studied. Additional research will be required to address this issue.

The standing crop biomass figures we estimated for the Mojave River are close to the mean reported for other semi-aquatic turtle species. Iverson (1982) estimated standing crop biomass for a multitude of turtle species from around the world. Mean maximum biomass for nine semi-aquatic species (including *C. marmorata*) was 19.2 kg/ha, near the low end of our estimate.

The reproductive ecology of our turtles is similar to that reported for other populations, including the possibility that Mojave River turtles produce multiple clutches in a given year, as has been reported elsewhere (Goodman, 1997). Circumstantial evidence suggests that two of our females produced double clutches in 1999. One female had four shelled eggs when X-rayed on 23 June and three when X-rayed on 14 July. Alternatively, she may have laid a single egg between X-rays. Another female was palpated and found to contain eggs on 11 June and 7 July, but none when palpated between those two dates.

Perhaps the most interesting difference between *C. marmorata* populations in the Mojave River and others is the limited terrestrial activity of the former. Other than terrestrial nesting forays by females, and movements by one male and two females between ponds at Camp Cady (87 m, one way), *C. marmorata* in the Mojave River appear to be highly aquatic. This observation is in sharp contrast to that reported elsewhere within the range of the species. Holland (1994) observed that *C. marmorata* in southern California spend 1–2 months per year in terrestrial habitats, while some individuals in Oregon overwinter in terrestrial locations for up to 8 months.

Why does *C. marmorata* overwinter in terrestrial sites throughout its range as noted for populations on the central coast of California (Rathbun, Scott & Murphey, in press), northern California (Reese & Welsh, 1997), and Oregon (Holland, 1994)? Reese & Welsh (1997) suggested that terrestrial overwintering behaviour may be an adaptive response to winter flooding. Many of the streams and rivers occupied by *C. marmorata* are subject to high flows in the winter (Gasith & Resh, 1999) that could easily displace hibernating turtles many

**Table 2.** Summary of ecological and physical attributes of Mojave River and other *Clemmys marmorata* populations. In recognition of the wide distribution and variation of the species, this table is not intended to be exhaustive, but rather representative for comparison and contrast of the attributes listed

| Attribute              | Population                       |  | Summary reference                        |
|------------------------|----------------------------------|--|--|
|                        | Mojave River (this study)        | Other  |  |
| Max. body size males   | 15.5 cm                          | 21.0 cm <sup>a</sup>                                   | Holland (1994)                           |
| Max. body size females | 16.0 cm                          | 19.2 cm  | Holland & Bury (in press)                |
| Sex ratio (♂/♀)        | effectively 1:1                  | 1.7:1  | Ernst <i>et al.</i> (1994)               |
| Biomass                | 18.85–37.71 kg/ha                | to 137 kg/ha   | Ernst <i>et al.</i> (1994)               |
| Population density     | 46–92 turtles/ha                 | 214 turtles/ha   | Ernst <i>et al.</i> (1994)               |
| Nesting season         | May–July (eggs in x-radiographs) | April–August   | Ernst <i>et al.</i> (1994)               |
| Clutch size            | 3–6 eggs (mean = 4.46)           | 1–13   | Holland (1994)                           |
| Max. clutch frequency  | 2?                               | 2  | Goodman (1997)                           |
| Egg size               | 37.04 mm × 19.0–23.0 mm          | 31–38 mm × 20–24 mm                                    | Holland (1994)                           |
| Hatchling size         | 25.6–27.9 mm                     | 25–31 mm   | Holland (1994)                           |
| Terrestrial activity   | nesting, overland dispersal??    | nesting, estivation, overwintering, overland dispersal | Holland (1994), Holland & Goodman (1996) |

<sup>a</sup> Specimens in southern California rarely exceed 16.0 cm (Holland, 1994)

miles downstream. The Mojave River is no exception in this regard, although high flows are usually associated with El Niño/Southern Oscillation events that do not occur on an annual basis. The apparent absence of terrestrial hibernacula use on the Mojave River suggests that factors other than flooding, perhaps extreme aridity of the surrounding uplands or predation, affect the hibernation behaviour of *C. marmorata*.

Another interesting contrast we observed was the great distance that most nesting females moved away from water at Camp Cady, bypassing potential nest sites on the pond margins in most cases, into the dry channel of the Mojave River. The single confirmed nest was just inside the drift fence and was likely an artifact of confinement. However, the majority of nesting movements took females well away from the pond margins. Long nesting movements are not unknown in this species with a very small percentage of females moving up to 402 m from water to nest (Holland, 1994). However, Holland (1994) and most previous studies indicate that the majority of females nest well within 50 m of water (Rathbun, Siepel, & Holland, 1992; Reese & Welsh, 1997). The strategy adopted by coastal populations of *C. marmorata* involving nesting away from streams may protect overwintering hatchlings from being scoured from the nest during winter floods (Rathbun *et al.*, 1992). Females at Camp Cady were often more than 100 m away from the ponds when they were suspected of nesting. However, the putative nest sites were on low sandbars in the flood plain of the Mojave River; areas that would be at risk to flooding according to the hypothesis proposed by Rathbun *et al.* (1992).

We speculate that Camp Cady females are returning to traditional nest sites and that the strategy of nesting in the flood plain was formerly adaptive in populations along the Mojave River. Prior to excessive ground water

pumping in the Mojave River, *C. marmorata* lived in the main channel of the river, not the ponds they currently occupy. Nesting on sandbars would have traditionally placed nests in close proximity temporally and spatially to high water levels during hatchling emergence. The use of sandbars for nesting is not unusual for this species when found in large rivers, as noted by Storer (1930).

Winter rains in this part of the Mojave Desert typically fall from December–March. Since hatchlings of this species are known to overwinter in the nest, presumably emerging as early as March of the year following oviposition in California (Buskirk, 1990; R. Fisher, pers. comm.), they may have been dispersed by floods in the Mojave River. The strategy of nesting so that hatchling emergence is coincident with high water levels and proximity to the waterline is used by a diversity of mostly tropical turtle species worldwide (e.g. *Podocnemis* spp., Pritchard & Trebbau, 1984; *Carettochelys*, Webb, Choquenot, & Whitehead, 1986; *Chelodina rugosa*, Kennett, Christian & Pritchard, 1993). With the drying of the river by excessive use of ground water for human activities, turtles were confined to the artificial ponds at Camp Cady, and the floods now come only rarely. Consequently, habitat alteration forces hatchlings to emerge from their nests at comparatively great distances from the remaining aquatic habitats (ponds). Hatchlings emerging from these distant nests are expected to experience greater energy expenditures and greater risk of predation or exposure while moving back to the ponds, than are hatchlings from nests closer to water (Congdon *et al.*, 1987), especially in the arid Mojave Desert.

The difference in adult sex ratios between our study and others is not unusual in comparisons with populations of turtles. Sex ratios in turtle populations are complex and vary according to sampling biases, envir-

omental sex determination of hatchlings, differential mortality of the sexes, differential immigration/emigration of the sexes, and differences in the timing of maturity between the sexes (Lovich & Gibbons, 1990). The small size of our sample and the influence of a multitude of factors on sex ratios limits additional comparisons.

According to the fossil record, *C. marmorata* had a much wider distribution in the Pliocene and Pleistocene. As the climate became dryer about 10 000 YBP, the range contracted and shifted farther to the west along the Pacific coast (Brattstrom & Sturn, 1959). Relict populations remained in the deserts of western Nevada (Banta, 1963), Baja California (Grismer & McGuire, 1993), and the Mojave River (Ernst *et al.*, 1994), until modern times. The late Pleistocene fauna of Lake Manix, the present site of Camp Cady, contained numerous fossils of aquatic species including fresh water molluscs, fish, birds, plants and *C. marmorata* (Jefferson, 1987), most of which are no longer found in the area. The occurrence of *C. marmorata* in the prehistoric Mojave Desert is further substantiated by the presence of shell fragments at numerous archaeological sites (Schneider & Everson, 1989). With the end of the cooler and moister regime in the Mojave Desert region between 8000 and 7000 YBP (Grayson, 1993), and the concomitant rapid disappearance of shallow lakes and marshes like Lake Manix (Meek, 1989), populations of *C. marmorata* became isolated in the Mojave River.

The relict status of *C. marmorata* in the desert of Baja California is also well-established. Grismer & McGuire (1993) listed *C. marmorata* as part of the relict mesophilic fauna of the oases of central Baja California. The transformation of that region from mesic to xeric was a gradual process becoming more abrupt about 10 000–8000 YBP. Because of the requirement of *C. marmorata* for access to aquatic habitats during a significant part of the year, it is highly unlikely that individuals naturally dispersed across the broad expanses of desert habitat that were created following the wetter Pliocene. Instead, the data suggest that this and other mesophilic species became isolated with desertification of south-western North America during the Holocene.

When considering the ecological and behavioural attributes we examined, populations of *C. marmorata* in the Mojave River exhibit few obvious adaptations to living in the desert and appear to be as dependent upon water as desert fishes. The general lack of ecological differences between desert and non-desert populations is probably related to their recent geographic separation (Brattstrom & Sturn, 1959). As such, desert populations are Pleistocene relicts and many of the traits exhibited by coastal populations of this wide-ranging species are a likely result of adaptations accumulated during a comparatively long period of residence in the Great Basin. The preservation of relict populations of *C. marmorata* in the Mojave River will require a commitment to protecting the water that allowed the species to survive in such a hostile surrounding environment.

### Conservation implications

Despite a long history of occupation in the Mojave River, modern populations of *C. marmorata* along the Mojave River were characterized as small and dwindling by Brattstrom & Messer (1988) and Buskirk (1990), an appraisal that our research supports. The Mojave Desert ecosystem has been dramatically altered by human activities (Lovich & Bainbridge, 1999) and the future health of the Mojave River system is in question, as is the survival of relict populations of *C. marmorata* and other obligate riparian species.

Most of the native riparian vegetation along the Mojave River was cleared for agricultural, residential and other uses, starting with the early settlers. As of 1995, only about 4047 ha of riparian vegetation remained, and about 648 ha showed signs of stress (Lines & Bilhorn, 1996). Ground water pumping lowered the water table in many areas causing increased mortality of native riparian vegetation (Lines & Bilhorn, 1996; Lines, 1999), a trend that is likely to continue as human populations increase in the urbanizing west Mojave Desert.

Where water remains on the Mojave River, invasion and spread of the woody shrub saltcedar, is a major problem. Introduced into the south-western United States from Eurasia in the 1800s (Lovich & de Gouvenain, 1998), saltcedar spread through riparian systems rapidly. In 1995, saltcedar was the dominant plant species in about 2104 ha of riparian vegetation along the Mojave River (Lines, 1999). Saltcedar infestation profoundly effects the geomorphology and hydrology of riparian systems, trapping and stabilizing alluvial sediments causing a reduction in channel width. Additionally, saltcedar groves have large water uptake and evapotranspiration rates and the longer a plant community is occupied by saltcedar, the more xeric the area becomes. Heavy infestations have actually been documented to lower local water tables. The net result of these changes is a river channel that bears little resemblance to a natural desert riparian system (Lovich *et al.*, 1994; Lovich & de Gouvenain, 1998). The ultimate consequence of these changes on riparian wildlife is difficult to predict but a decreasing supply of water certainly places *C. marmorata* populations at risk.

An additional risk is presented by a major rail line that parallels the Mojave River for most of its course through the desert, crossing the river at several points, including Afton Canyon. The proximity of trains to the riparian system provides the potential for toxic spills from wrecks. Both spills and illegal dumping of toxic materials have occurred at Afton Canyon in the past (T. Egan, pers. comm.). Bury (1972) documented the lethal effects of a diesel spill on a stream fauna in northern California, including *C. marmorata*. This was not an isolated incident as similar spills have exposed *C. marmorata* populations to toxic substances at other locations in California in recent years (Luke & Sterner, 2000). Effective spill response procedures would need to be implemented to protect turtles if a spill occurred in or near Afton Canyon.



Given the tenuous status and small size of *C. marmorata* populations in the Mojave River, immediate conservation action is suggested. Establishment of satellite populations should be considered as a hedge against extirpation of these relict populations.

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