Predator-proof field enclosures for enhancing hatching success and survivorship of juvenile tortoises: A critical evaluation

Kristin Highberg Berry
United States Geological Survey

Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles—An International Conference, pp. 147–165

Predator-Proof Field Enclosures for Enhancing Hatching Success and Survivorship of Juvenile Tortoises: A Critical Evaluation

DAVID J. MORAFKA,[1] KRISTIN H. BERRY,[2] AND E. KAREN SPANGENBERG[1]

[1]*Department of Biology, California State University, Dominguez Hills, Carson, CA 90747-0005, USA [email: papaherp@aol.com]*
[2]*U.S. Geological Survey, Biological Resources Division, 6221 Box Springs Blvd., Riverside, CA 92507-0714, USA*

ABSTRACT: *In situ* predator-proof enclosures or pens can provide low-cost technology to conduct research on early life stages of tortoises and improve hatching success and juvenile survivorship of threatened and endangered species without the negative effects commonly experienced with captive-reared tortoises.

***In situ* experiments with two North American tortoise species, the Bolson tortoise (*Gopherus flavomarginatus*) and the desert tortoise (*G. agassizii*), provided valuable insights. The initial work (1983) with *G. flavomarginatus* at Mapimí, Durango, Mexico was characterized by extensive human manipulation and relatively low survivorship. Eggs were harvested from wild females using injections of oxytocin and were hatched in outdoor solar-powered incubators with a 65–67% success rate. Neonates were transferred to 20, 1 × 3 m wood and adobe pens constructed within an 11 × 13 × 2.5 m outdoor wire enclosure. Each pen held 1–2 neonates, which were provided with water and food. During the three-year trial, survivorship in the nursery was 76% (n = 86). Annual growth rates of juveniles declined from 184.7% (in weight) in the first year to nearly zero in the third year. For the 1983 cohort of neonates, three-year survivorship was 60%.**

Building on the experience of the 1983 project, a second, but more passive, program was initiated in 1990 for *G. agassizii* at Fort Irwin in the Mojave Desert of California, USA. Wild females were temporarily relocated to a 60 × 60 × 2.6 m high fenced enclosure with natural, undisturbed desert vegetation. Females were permitted to range freely and nest, after which most were returned to their home sites. Hatching success was 90–94%. Some neonates constructed their own burrows, while others exploited pre-existing shelters or artificial burrows. No food or water was provided. Most individuals showed continuous growth into the third year. Drought conditions were probably responsible for declines in their growth and weights in the fourth year, and by the end of the fifth year, five (4.5%, n = 110) juveniles had died of starvation and dehydration. Excluding juveniles killed by predators (in a control area and in an exposed section of the enclosure), overall survivorship for the first three and one half years (between 1990 and 1994) was 88%. Despite the losses to drought during the fourth and fifth years, this passive treatment shows greater promise of success. The issue of carrying capacity within an enclosure, however, requires further investigation. Designs for two different field enclosures and alternate treatments are proposed, and recommendations are made for future *in situ* field programs.

Most hatchery and nursery operations undertaken to conserve chelonians have focused on sea turtles (Bjorndal, 1982) as well as some species of freshwater turtles. Because aquatic turtle nests are often aggregated, eggs and neonates can be located and protected more easily than those of terrestrial turtles and tortoises. Projects intended to protect eggs and neonates of aquatic chelonians subsequently developed into extended programs to raise juveniles to sizes that were less vulnerable to predation. Designed to counterbalance increasing losses to predators, habitat degradation, or habitat elimination, such intervention programs have been called "headstart efforts" (Carr, 1984).

Like the aquatic turtles, the majority of terrestrial chelonians are threatened by both direct human take and anthropogenic degradation of their ecosystems. In contrast to many species of aquatic turtles, however, testudinids and terrestrial emydids rarely have concentrated or communal nesting sites (Moll, 1979; Mrosovsky, 1983; Swingland and Klemens, 1989).

Yet after 30 years of intermittent sea turtle headstart programs, there is little evidence that progeny from hatchery and nursery programs survive to reach breeding age. Some authors (e.g., Mrosovsky, 1983; Frazer, 1992) have given negative reviews of these intervention programs. Frazer (1992, this volume) identified five areas of criticism. First, artificial propagation of young may be rendered ineffective unless the original causes of population declines are eliminated. In Frazer's classic example of sea turtles, habitat degradation from oil spills and global warming and loss of adults to shrimp nets could not be compensated by the "half-way technology" of simply producing more juvenile turtles for release into environments no longer able to sustain them. Second, headstart operations can perpetuate themselves as self-serving sociopolitical institutions that are attractive to a naive public. Such endeavors are often inaccurately equated to livestock husbandry. Third, evaluations of the efficacy of hatcheries and nurseries are often deferred for a generation, because only successful reproduction is a valid determinant of the survivorship to adulthood of the released juveniles. Fourth, the normal and appropriate roles of eggs and juveniles as prey in the context of food webs may be diminished by hatchery and nursery operations (Frazer, 1992). Erosion of gene pool diversity and heterozygosity may also result when a few females provide almost all progeny for the F_1 generation. Rarely do effective population numbers reach the hypothesized requisite of 500 reproducing adults (N_e) necessary to minimize inbreeding depression and drift-related losses in genetic diversity (Lande and Barrowclough, 1987). Fifth, hatchery efforts also direct conservation efforts to juveniles, which individually have the lowest probability of contributing to recruitment, rather than to reproductive adult females, which have the highest.

Mrosovsky (1983) provided three additional pragmatic considerations: Captive-reared juveniles released into natural surroundings may suffer spatial disorientation, lack wariness of predators, and be conditioned to inappropriate food items. In addition, the artificially elevated densities in captive chelonian colonies may result in malnutrition and epidemic disease.

It should be noted that the tactics and technology of headstart programs have evolved considerably over the last three decades: Nutrition has been improved, which promotes more normal growth; holding centers provide better hygiene and more space to accommodate growth and activity; longer rearing periods permit the release of larger turtles, which are less vulnerable to predators; the use of TEDs has reduced incidental take; in some marine habitats local pollution may have abated sufficiently to reduce environmental loss; and public education may also reduce losses to human activities. Given sea turtle generation intervals, however, it may be at least another 20 years before headstart programs receive a full and impartial evaluation.

During the past decade, headstart technologies developed for sea turtles have been modified for terrestrial chelonians. In this paper we evaluate field-based enclosures both as hatcheries and nurseries for restocking threatened and endangered tortoises and as research tools for obtaining more data on life history attributes.

Definition of Field Enclosures

At minimum, a field enclosure is a fenced area of suitable habitat on or within the historic range of the particular species and is capable of physically housing at least one clutch of eggs and sustaining the resulting neonate tortoises. (Neonate here refers to a juvenile <1 year of age and for which age is absolutely known, e.g., through mark-recapture data, Morafka, 1994.) The site need not sustain young tortoises for any particular time period beyond hatching and emergence. The individual tortoises need not be drawn from the local surrounding habitat. This core definition can include interventions as simple as a small cone or "tent" (sufficient to sustain the neonates from a single clutch for one season) or as complex as a field hatchery for hundreds of eggs with fenced pens extending over several hectares. We focus here on the larger and more complex structures used as hatcheries and nurseries. Most projects have been directed toward restocking or reintroduction.

Other Testudinid Hatchery and Nursery Programs that Utilize Enclosures

In the last three decades, at least a dozen hatchery and nursery operations have been proposed or implemented for 11 taxa of tortoises (Table 1) in 12 wild or semi-wild settings within or bordering on historic geographic ranges. The limited number is understandable, considering logistical difficulties, costs, and lack of critical life history data for many species. Purposes for the facilities vary considerably and range from raising highly endangered species for restocking, translocation, or repatriation into natural and historical habitats to providing holding facilities for captives. One important function in North America continues to be the gathering of scientific data on survivorship, behavior, physiology, and health of wild-raised tortoises, even when locally robust populations render restocking unnecessary. Education of local residents and visitors has also been incorporated into some programs, and one program for *Aldabrachelys elephantina* (formerly *Geochelone gigantea*) on Curieuse Island was established in part to provide a tourist attraction and deflect tourist pressure from the atoll of Aldabra (Stoddart et al., 1982; Hambler, 1994). At least one program (for *Geochelone sulcata*) in western Africa was designed to provide food for human consumption (IUCN/SSC, 1989). The best known, longest-term, largest, and most successful operation is for *G. nigra* in the Galápagos Islands (McFarland et al., 1974; Cayot et al., 1994; Cayot and Morillo, this volume). The program has singlehandedly saved *G. n. hoodensis*, of which *all* wild specimens at present were headstarted and are now breeding. Other hatchery and nursery programs (e.g., for *Geochelone radiata*) have been established at zoological parks and reserves outside the historic geographic ranges of species.

Two Case Studies in North America

Two studies of field enclosures for the Bolson tortoise (*Gopherus flavomarginatus*) and the desert tortoise (*G. agassizii*) are presented below. The *G. flavomarginatus* program was actively managed, whereas the *G. agassizii* program, drawing upon the experiences of the former, used a passive strategy. The purposes of the two projects and ecological and societal contexts in which they existed also differed substantially.

The Mapimí Site

Purpose of the Project. The first long-term tortoise enclosure was established in North America in 1983 by Mexico's Instituto de Ecología at its Laboratorio del Desierto in the state of Durango to (1) provide baseline data on life history attributes, and (2) attempt to enhance recruitment in local populations of the Bolson tortoise, an endangered endemic species confined to the Bolsones (closed basins) de Mapimí of Mexico's central Chihuahuan Desert. Artificial enclosures were established because few young tortoises were observed during early studies (Legler and Webb, 1961), and 20 years later only captive juveniles were available to characterize juveniles and their growth (Morafka, 1982). A critical component of this project was the active involvement of local residents who were employed in the construction and maintenance of the physical enclosure and in care and maintenance of the juvenile tortoises. This was a labor-intensive endeavor in which a small space was managed and supplemented by human effort.

Location and Description of the Study Site. Situated in the endemically rich Mapimían Subprovince of the Chihuahuan Desert (Morafka, 1977), the vegetation is a patchy distribution of thorn scrub on a 2–3% grade (Martinez and Morello, 1977; Morafka et al., 1981). Dominant and important plant species are creosote bush (*Larrea tridentata*), prickly pear cactus (*Opuntia rostrata*), mesquite (*Prosopis glandulosa*), tar bush (*Flourensia cernua*), tobosa grass (*Hilaria mutica*), mallow (*Sphaeralcea angustifolia*), and grama grass (*Bouteloua* sp.).

The hatchery, nursery, and adjacent release site were in the Mapimí Reserve 26°29′–26°52′ N, 103°32′–103°58 W at 1,100 m approximately 1 km NE of the Laboratorio del Desierto field station in Durango, Mexico (Tom, 1994).

The Local Tortoise Population. Local populations tend to be dominated by adults and neonates with low percentages in intermediate age classes (Adest et al., 1989a). Aguirre et al. (1984) suggested that high density population clusters may reach 300 adults/km², whereas more widespread, low density areas would average approximately 10 adults/km².

Parental Stock and Handling of Eggs. Healthy, free-living adults served as parental stock (Morafka et al., 1986). Gravid females collected from a wild population 10 km NW of the Laboratorio were the source of eggs. Carotid and axillary blood samples were taken, and hematologic and serum biochemistries indicated no particular health problems, but fecal samples revealed high ascarid (nematode) egg counts. Such parasite loads are not necessarily detrimental to health as nematodes may serve as detritivores (shredders) in facilitating digestion (as suggested for iguanines by Iverson, 1982).

Presence of eggs was determined by inguinal palpation. Some females were induced to deposit their clutches by an intramuscular injection of oxytocin at a dosage of 1.0 USP unit/kg of body weight, whereas some laid eggs without artificial stimulation (Adest et al., 1989b).

Three incubation designs were utilized: (1) a constant temperature-controlled water-bath incubator (30°C), with eggs in cardboard trays; (2) eggs partially buried in sand in a wood box enclosure with ambient fluctuating temperatures (22–37°C); and (3) eggs incubated outdoors in nests naturally excavated in soil (protected only by the courtyard walls of the institute). Incubation required from 95 to 115 days, depending on the date of deposition, type of incubation, thermal regimes, and other factors (Adest et al., 1989b; G. Aguirre, pers. comm.).

Hatching Success. Hatching success, when completely infertile clutches were excluded from the calculations, averaged 65–77% (Adest et al., 1989b).

Raising Juvenile Tortoises. The enclosure, measuring 11 × 13 × 2.5 m high, was constructed of adobe and wood and was covered with 13 mm chicken wire mesh (Adest et al., 1989b). In its first year of operation, the enclosure was stocked with freshly hatched neonates and with one-year-old individuals previously maintained in terraria. Ten stalls, each 1 × 3 m and facing west, were divided by wood partitions and were backed by an equal and opposite set facing east. Each stall was entirely separated from adjacent stalls with 1 × 3 m wood partitions. Insulation cloth covered the back third of the enclosure to provide shade. Each stall was equipped with a pre-excavated burrow (approx. 30 cm long) and a shallow water dish (approx. 20 cm in diameter × 5 cm deep). Each pen held 1–2 tortoises. A single door with a lock provided access to the entire unit.

Growth Rates of Juveniles. All nursery-raised tortoises were provided with water and fed hand-cut and stored native grasses and forbs when available (*Hilaria mutica*, *Bouteloua barbata*, *Eragrostis intermedia*, *Solanum elaeagnifolium*, *Sphaeralcea angustifolia*), or dried baled alfalfa when native plants were unavailable between November and June (Adest et al., 1989b). The selection of native grasses and forbs was based on the known diet of adults.

Growth data are available for the first cohort (n = 23) of neonates from 1983 (Adest et al., 1989b). Carapace length (CL) and weight increased an average of 48.8% (SD ±5.7)

TABLE 1
A global survey of tortoise species for which breeding programs have been established in wild or semi-wild settings, or are proposed for restocking of native habitats.

Species	Location	Type of program	Reference
North America			
Gopherus agassizii	National Training Center at Ft. Irwin, California, USA	Two semi-wild, predator-proof enclosures for nesting females and raising of hatchlings and neonates. Minimal manipulation of eggs, neonates, and juveniles.	Joyner-Griffith, 1991; Morafka, 1994
G. flavomarginatus	Mapimi, Durango, Mexico	Incubators and predator-proof nurseries; considerable manipulation of females, eggs, neonates, and juveniles.	Morafka et al., 1986; Adest et al., 1989a, 1989b
South America			
Geochelone nigra hoodensis	Charles Darwin Research Station (CDRS), Galápagos Islands, Ecuador	A wide variety of actions, including nest protection in the wild; eggs removed to CDRS for hatching, raising of young, and restocking of wild populations. Approach by specific populations or races. *G. n. hoodensis* is the only ssp. captive bred, but several other species are headstarted.	MacFarland et al., 1974; Cayot et al., 1994; Cayot and Morillo, 1997
Europe			
Testudo h. hermanni	La Station D'Observation et de Protection des Tortues des Maures (SOPTUM), Gonfaron, France	A mix of captive breeding as well as management of wild tortoises; a large restocking effort. The last remaining Hermann's tortoise population in mainland France.	Stubbs, 1989b; Devaux and Stubbs, 1997
T. h. hermanni	Northeastern Spain	Captive breeding center.	Mascort, 1997
T. h. boettgeri	Port-Cros National Park and Porquerolle, France	Two rearing trials in enclosures; 150 tortoises released on island.	Cheylan, 1984
Testudo graeca	Elche, Alcante Province, Spain	A private facility, goal of reintroductions to the wild.	Stubbs, 1989a

Species	Location	Type of program	Reference
Sub-Saharan Africa			
Geochelone sulcata	Nazinga Ranch, Burkina Faso, Sudan	Small-scale captive breeding program to evaluate potential for meat production; potential pilot project for reintroduction of tortoises to Sudan using stock from Al-Ain Zoo, Abu Dhabi.	IUCN/SSC, 1989
Indian Ocean—Madagascar			
Geochelone yniphora	Ampijoroa Fortestry Station, Madagascar	In 1985, the IUCN/SSC Tortoise Specialist Group in collaboration with the WWF-International Jersey Wildlife Preservation Trust initiated a recovery program for relocating and breeding tortoises.	Curl et al., 1985; Durrell et al., 1989c; IUCN/SSC, 1989
Geochelone radiata[a]	Ivolohina; Parc Tsimbazzaza; Réunion Island	Groups of tortoises at three sites; several groups introduced on Réunion, where breeding occurs naturally.	Durrell et al., 1989b
Acinixys (Pyxis) planicauda	Ampijoroa breeding facility, Madagascar	Identified need and proposal to expand breeding facility at the Ampijoroa Forestry Station for site captive rearing and protected breeding.	Durrell et al., 1989a; IUCN/SSC, 1989
Indian Ocean—Aldabra Island			
Aldabrachelys elephantina (fomerly *Geochelone gigantea*)	Curieuse Island, Seychelles	Operation Curieuse: 299 Aldabran giant tortoises introduced to Curieuse Island to establish a second (reserve) population. Purposes: tourist attraction to deflect tourism from Aldabra, monitor growth and demography, re-establish tortoises recently lost to central Seychelles, use new population to supply zoos overseas, and meet local demand for domestic tortoises.	Stoddart et al., 1982; Swingland, 1989; IUCN/SSC, 1989

[a] Does not include the successful colonies of the Wildlife Conservation Society's breeding herd at St. Catherines Island, Georgia, USA (1981–). This program is outside the historic geographic range.

and an average of 184.7% (SD ±37.9), respectively, in the first year (n = 23). By the second year, 19 of the 23 first-year tortoises remained. For the 19, CL increased an average of 19.8 mm (SD ±4.5) or 29.5% (SD ±5.5), and weight increased an average of 77.0 g (SD ±29.4) or 108.4% (SD ±19.8) during the second year. By the third year, growth rates declined to an average of 0.2 mm (SD ±0.4) CL, and the average weight increment was only 1.8 g (SD ±3.7) for the eight tortoises for which data were available. Third-year values are effectively zero when SD and sampling error are considered.

Status of Health. Some juveniles in the enclosure showed signs of illness. Third-year juveniles failed to grow, and the majority of second-year and third-year tortoises developed pyramiding carapaces and knobby plastrons (Adest et al., 1989b). Knobby carapaces have been described in cases of severe nutritional osteodystrophy due to a calcium-deficient diet (Jackson and Cooper, 1981). Such conditions compromise shell hardness and probably reduce long-term viability. After nutrient deficiencies were suspected in 1985, the natural diet was analyzed by fresh plant parts rather than by species (Adest et al., 1989b). Human caretakers had provided the young tortoises with forage from dried bundles of whole native grasses and locally grown alfalfa. Analyses of these and similar dried whole mature grasses yielded only 3.5–8% protein whereas immature fresh green shoots, preferred by juvenile tortoises, averaged approximately 16% protein (Adest et al., 1989b). Studies of another chelonian, *Trachemys scripta,* have indicated that higher protein (≥ 16%) diets are critical to sustain normal growth in juveniles (Parmenter and Avery, 1990). After 1985 the protein and mineral content of the young tortoises' diet was enriched by feeding fresh-cut alfalfa, and in subsequent cohorts and year classes shell abnormalities were reduced and new growth was sustained.

Survivorship and Causes of Death. In 1985, 86 living neonate and juvenile tortoises remained from the three cohort years of 1983, 1984, and 1985. The combined survivorship for all three cohort years is 76% (Adest et al., 1989b). Survivorship was 60% for the 1983 cohort year, 55% for the 1984 cohort year, and 86% for the 1985 cohort year.

Tortoise deaths (n = 21) were attributed to six causes: 7 (33%) from decalcification and desiccation, (probably from malnutrition); 6 (28.6%) from either drowning in water dishes or prolonged insolation after being overturned while attempting to climb the wood dividers separating the stalls; 1 (4.8%) from exposure to cold; and 7 (33%) from undetermined causes.

Survivorship after Release. In 1986 ten neonate tortoises, hatched from the passive solar incubator and held ≤18 days, were released in August and September to the wild (Tom, 1994). Only four of the ten were still alive 11 months after release.

The Fort Irwin Study Site (FISS)

Purpose of the Project and Enclosure. In 1990 a field enclosure was constructed at the National Training Center (NTC), Fort Irwin, California, for a population of the threatened Mojave Desert tortoise (USFWS, 1994; Joyner-Griffith, 1991). This study population was robust both in absolute numbers and in age class representation. The objectives for the enclosure were twofold: to gather baseline data on life history attributes of juveniles and to determine survivorship of released juveniles. Restocking the general area was not an objective. The new enclosure was 60 times larger than the enclosure for the Bolson tortoise, it was remote from human populations, and it was serviced only twice a month. The enclosure was assumed to have a carrying capacity sufficient to sustain the confined and protected juveniles with minimal human intervention.

Location and Description of the Study Site. The Fort Irwin Study Site (FISS) is on the SE corner of the U.S. Army's NTC at Ft. Irwin, approximately 15 km NW of Afton Canyon, San Bernardino County, California (35°06′ 49″ N, 116°29′27″ W, 650 m elev.). Two enclosures, FISS I and FISS II, are situated on 2% slope of NE-facing sandy hillsides, which are cut by dry washes draining east to West Cronese Dry Lake. The soil surface is stabilized by a well-developed desert crust. Vegetation is Mojave Desert creosote bush scrub (Vasek and Barbour, 1988), specifically big galleta shrub steppe (USFWS, 1994) dominated by creosote bush and white bursage (*Ambrosia dumosa*), with other common shrubs including *Lycium pallidum* and *Ephedra nevadensis*. The native bunch grass galleta, *Pleuraphis rigida*, is common despite the intrusion of Mediterranean annual grasses such as *Bromus madritensis* ssp. *rubens* and *Schismus barbatus*. The study site, which has not been used for military training or comparable activities, is protected within the confines of the NTC and remains one of the most pristine landscapes in the region.

The Local Tortoise Population. The study population is part of the Superior-Cronese Desert Wildlife Management Area (USFWS, 1994), with densities of local tortoise populations estimated at an average 19 adults/km² (range 8–97 adults/km²).

Description of the Enclosure. The enclosure was constructed in a manner that would conserve the natural vegetation and limit disruption of the natural crust of desert soil. The 60 × 60 m area is enclosed by chicken wire fencing and roofing, supported by 2.6 m poles anchored in concrete. The perimeter of the enclosure is bounded by 1 cm mesh hardware cloth buried 0.76 m deep and continued 0.6 m above ground to exclude small vertebrate predators. The unit is divided into northern and southern sections by a 2 m high chicken wire fence. The frames of the two locking entrance doors have 10 cm raised sills to confine juvenile tortoises should the doors be left ajar.

When first constructed in May 1990, chicken wire roofing was installed over only the northern half of the enclosure. After an attack by avian predators (probably the common raven, *Corvus corax*) in May 1991, roofing was installed over the southern half by July 1991. Midway along the southern fence a bamboo blind (approx. 3 m wide × 2 m tall × 2 m deep) permits young tortoises to be observed without disturbance from human movements or shadows. A solar-powered Campbell Scientific Instrument weather station, located at the southwest corner of the site, records air and soil temperatures, wind velocity, and precipitation every 15 minutes and downloads the data to a remote computer at designated intervals by cellular phone.

Neonates were free to roam the 60 × 30 m subdivision in which they were hatched. Most (83%) constructed their own burrows within a few days of hatching, whereas others used abandoned rodent burrows or shared artificial burrows that had been constructed for adults (0.25 m wide × 1 m long beneath 0.5 m of soil) (M. Joyner, pers. comm.). Researchers and occasional visitors walked through the enclosure to collect data on tortoises, and created a network of small trails and trampled soils.

Source and Handling of Eggs. Each May from 1990 through 1993, 8–10 adult females were collected from the surrounding 5 km^2, and their field sites were recorded. Gravid females were identified by radiograph and placed in the enclosure to nest virtually undisturbed. Non-gravid females were immediately returned to their original field sites. After depositing their eggs, most of the remaining females were also returned to their original field sites. Typically, two females were retained in the enclosure to generate fresh feces for ingestion by fall neonates (Dezfulian et al., 1994). To avoid mechanical disturbances that might compromise hatching success, nests were not examined.

Hatching Success. Neonate tortoises emerged 85–110 days after egg deposition. The incubation period was estimated by starting with the week in which eggs were first absent from radiographs of previously gravid females. Radiography was conducted at the field site to minimize disturbance to nesting females. Females were moved no more than 50 m during the 15-minute examination procedure, which occurred no more often than once per week. The rate of hatching (based on radiographs of gravid females and fall 1990 capture records of neonates) was estimated at 90–94%, which is substantially higher than the 46% reported by Turner et al. (1986) for eggs relocated from natural deposition sites to predator-proof nests.

Sex Ratios. Twenty-nine tortoises hatched at FISS, ranging in age from three to five years, were sexed in 1995. Twenty-four males, five possible males, and ten females suggested a three-to-one sex ratio (Lance, 1995). This significantly skewed finding ($P < 0.05$) contrasted with the 1:1 ratio reported as typical for natural populations (Dodd, 1986). Populations with sex ratios highly skewed toward males have been considered to be in poor condition (Berry, 1976).

Growth Rates of Neonates and Juveniles. The length and weight increased an average of 8.7% (SD ±3.9) and 21.7% (SD ±16.5), respectively, for all age classes (first- to third-year tortoises) pooled during the 1993 growing season, a year which had above-average rainfall. However, in 1994 when annual precipitation was 70% below average, no increase in CL occurred, and weight decreased by an average of 25% (SD ±6.5). With above-average rainfall in spring 1995, weights of juveniles increased an average of 70% compared with the lowest values recorded in 1994.

Neonates and Juveniles Released from the Enclosure. In March of 1991, 12 neonates were fitted with radio transmitters and released from the enclosure to the surrounding area. Juvenile tortoises have been monitored since 1991 on a quarterly (seasonal) or triennial basis for external signs of disease, evidence of fecal parasites, and blood chemistries and peripheral blood cell counts obtained by axillary samples or cardiocentesis. Some individuals showed elevated values for blood urea nitrogen (BUN) and uric acid levels during the driest sampling periods. These elevated values are indicative of episodic dehydration (R. Yates, pers. comm.; Christopher et al., this volume). While abnormal blood cell counts were rarely observed, clinically normal animals occasionally displayed mild leukocytosis or mildly depressed packed-cell volumes (Morafka, 1993). No abnormal loads of parasites or bacteria were reported, though the potentially mutualistic fermenting anaerobe, *Clostridium bifermentans*, was isolated (Dezfulian et al., 1994).

Survivorship and Causes of Death. Sixty-eight percent ($n = 162$) of neonates and juveniles have survived 1–5 years. In May of the first year (1991) 18 of 24 juveniles occupying the unroofed southern enclosure were lost to avian predators, probably the common raven (Morafka, 1993). This first year survivorship does not differ significantly ($P > 0.05$) from that reported by Tom (1994). Eight of 12 free-ranging, control group juveniles, fitted with radio transmitters, were similarly preyed upon at this time. If these avian predation numbers are excluded, overall survivorship rises to 76%. In comparison, Turner et al. (1987) reported a similar but higher annual survivorship of 76.7% for juveniles <60 mm CL, 79.5% for juveniles 60–79 mm CL, and 80.4% for juveniles 80–99 mm CL (figures are for geometric annual means) in a wild population in the eastern Mojave Desert for periods spanning nine years. These high survivorship values suggest that interventions may not provide significant advantages except in unusual situations, e.g., when local ravens or other predators are increasing the rates of predation or where interventions significantly reduce nest predation by foxes.

Annual survivorship from fall 1993 to spring 1994 for all age classes (first through third years) pooled was 86%. In spring 1994 survivorship was greatest for the 1990 (age 3.5 years) and 1991 (age 2.5 years) cohorts at 88%. This three-year survivorship was significantly greater ($P < 0.05$) than 60% reported for the equivalent Mapimí cohort of enclosed tortoises. It decreased to 80% for the 1992 cohort and was only 50% for the 1993 cohort. In the 1994 drought growth rates and weights of juveniles declined. Five (4.5%) juveniles had died of starvation and dehydration by December 1994.

Population Density within the Enclosure. Juvenile tortoise densities increased annually with each newly hatched cohort. Densities inside the enclosure were the equivalent of 152/ha in 1990 and 344/ha in 1993 (Table 2). The numerical densities for juveniles within the enclosure are 300× to 900× the densities of wild juvenile and immature tortoises estimated by Berry (1990) using mark-recapture data for four nearby study sites in the western Mojave Desert (Table 3). Berry's density figures apply to a wider range of sizes and include immature tortoises up to 139 mm CL with estimated ages of 8–12 years. If Berry's density figures are adjusted for the younger and smaller tortoises found at FISS, the density of juveniles in the enclosure surpasses field estimates by factors of 50× to 100×.

Some behaviors exhibited by both juveniles and adults within the enclosure were aberrant, a possible indication of overcrowding. Thirty-five percent of FISS tortoises shared burrows with two or more tortoises, a pattern not observed in the wild for 1,403 juvenile and immature tortoises at 18 study sites in California (Berry and Turner, 1984, 1986). Juveniles that shared burrows frequently were observed to cluster in the entrances, preventing those inside from emerging and those outside from retreating into the burrow. Thus, the individuals outside the burrow were exposed to excessive temperatures. On one occasion, a small juvenile was observed to follow its larger burrow-mate through the shrub canopy to the burrow.

TABLE 2
Population density and survivorship of neonate and juvenile desert tortoises hatched and maintained in a semi-wild enclosure at the Fort Irwin National Training Center, San Bernardino, California.

	Estimated numbers of tortoises				
Cohort by year	1990	1991	1992	1993	1994
1990 Cohort	55	31	23–26	26–28	22–25
1991 Cohort	—	88	73–76	74–79	67–73
1992 Cohort	—	—	13	10–11	8–9
1993 Cohort	—	—	—	6	3
Totals	55	119	115	124	110
Density/ha	152	329	319	344	305

TABLE 3
Population densities of juvenile and small immature (<140 mm carapace length at the midline) desert tortoises at four sites in the western Mojave Desert of California. This size range includes tortoises from emerging neonates to individuals estimated at 8–12 years of age. Data from Berry, 1990.

Site name	Year	No. juvenile and small immature tortoises/ha (95% Confidence Interval)
Fremont Valley	1981	0.43 (0.36–0.53)
Desert Tortoise Natural Area interior	1979	0.75 (0.58–0.98)
Desert Tortoise Natural Area interpretive center (inside fence)	1979	0.44 (0.37–0.51)
Kramer Hills	1982	0.69 (0.54–0.87)

Adults placed in the enclosure to lay eggs and produce scats were observed to usurp juvenile burrows and enlarge them into pallets or adult burrows. Adults also visibly reduced the limited supply of desert annual plants available as forage.

Survivorship after Release to the Wild. Nine 3-year and 4-year juveniles were fitted with radio transmitters and released outside the enclosure in May 1994. Nine months later 66.7% were still alive.

Status of Health. The local tortoise population is robust, and intermediate age-size cohorts are well represented. In 1994, 20+ tortoises of various ages within and outside the enclosure were screened for antibodies to *Mycoplasma agassizii*, the pathogen responsible for infectious upper respiratory tract disease (URTD), using an ELISA test (Schumacher et al., 1993; E. Jacobson, pers. comm.). Four (7.7%) of 52 tortoises sampled between 1993 and 1995 were seropositive, and an additional six (11.5%) were suspect for *M. agassizii* (Jacobson et al., 1996). Of the four seropositive tortoises, three were adult females and one was a juvenile in the FISS enclosure.

Comparison and Evaluation of the Two *Gopherus* Hatcheries, Nurseries, and Release Programs

Both active and passive management approaches have advantages and liabilities and must be viewed as hypothesis-testing experiments. Neither management approach provides guaranteed recipes for hatching, rearing, and restocking young tortoises to the wild. Ecological and socio-economic contexts may determine which experimental approach is more appropriate. If it is cost-effective to utilize local resident caretakers and if the enclosure is small relative to the density of tortoises it is expected to maintain, an actively maintained enclosure may be justified. Active manipulation would also be favored at sites where weather conditions are too varied and production of forage is too uncertain for successful passive operation. An actively maintained (and closely monitored) enclosure may also be justified when poaching and/or vandalism would otherwise disable the effort. Conversely, a passive approach is justified if weather patterns, forage production, physical space, and soil provide consistently sufficient resources to support a high density of juvenile cohorts. At remote sites where humans are not resident and the risk of human interference low, the need for costly on-site caretakers is diminished, and a passive operation may be more appropriate.

Criteria for Defining and Developing Successful Tortoise Enclosures

Mrosovsky (1983, p. 25) stated the best criteria for judging success of headstarting in sea turtle programs:

"Perhaps the best—the ultimate—validation would be, after many years, a greater percentage of headstarted turtles among the breeding females than might be expected on the basis of the percentage of eggs taken for headstarting (Buitrago, 1981; Pritchard, 1981). For this it would be necessary to know not only how many eggs were taken for headstarting but also the percentage of the total laid that this take compromised."

His definition applies equally well to assessments of similar conservation efforts for tortoises. Determination of success could require 20 years of intensive monitoring, not only of specific cohorts but of the entire population. A very important milestone would be a demonstration of successful reproduction of a majority of the headstarted animals.

The Role of Enclosures in the Future

Tortoises may be better candidates for hatcheries and nurseries than many species of aquatic turtles because of their life history characteristics. Manipulation of tortoise eggs is often unnecessary, imprinting on ancestral nesting beaches is not an issue, conditioning to appropriate diets may be less critical for generally opportunistic herbivores (and for some omnivorous taxa such as *Kinixys*, Obst et al., 1988), and acquired skills at predator avoidance may be less critical for fossorial species that spend >95% of their lives in burrows. Furthermore, some tortoises live in terrestrial habitats that can be more easily managed, e.g., controlled burning to stimulate disclimax grassland in Florida forests for *Gopherus polyphemus* populations (Auffenberg, 1969; Diemer, 1986). We offer four applications of enclosures for tortoises in wild or semi-wild settings:

1. Augment recovery of "Threatened" and "Endangered" populations by adding annual cohorts of juveniles. Traditionally, biologists have assigned low values to neonates and juveniles because of their high assumed mortality rates (e.g., Auffenberg and Iverson, 1979). Despite the many difficulties inherent in hatchery and nursery operations, protected eggs and juveniles have the potential to accelerate recovery of threatened and endangered populations, especially if large cohorts can survive the early vulnerable years. From this perspective neonates and juveniles are the most important age classes for achieving rapid recovery. The 25-year program of successful hatching, nursery, rearing, and releases of Galápagos tortoises is a prime example of the benefits of such techniques (MacFarland et al., 1974; Cayot et al., 1994; Cayot and Morillo, this volume).

In some cases, while habitats have remained intact, tortoise populations have declined because of commercial uses, collection for pets or food, vandalism, disease, or subsidized native predators (Boarman, 1993). In the last case, native predators' numbers have increased to densities that exert abnormally high predation pressures on the tortoises. Predator populations often proliferate because their food sources are subsidized by urban and agricultural wastes and landfills. If specific threats can be eliminated, artificially enhanced hatching success and juvenile survivorship may prove to be an effective technology.

For species such as *Gopherus polyphemus*, evidence exists that recruitment in wild tortoise populations may be a highly stochastic process: A decade of reproductive effort may yield only one good year in which predation pressures on eggs and young are sufficiently abated, or production of forage elevated, to usher through a particular cohort of neonates (Landers et al., 1982). Accordingly, chelonian conservationists could employ *in situ* predator-proof enclosures to artificially suppress predation to create the equivalent of one or more good years to enhance or accelerate recruitment.

2. Collect data on life history attributes of difficult-to-find neonates and juveniles. Young tortoises in the wild are so elusive that if they were treated as a species separate from adults, they would be among the rarest and the least understood terrestrial vertebrates. Even for one of the most thoroughly studied species, *Gopherus polyphemus*, a review of the past 200 years of scientific literature revealed only five citations that addressed juvenile tortoise biology (Douglass, 1978). Similar but less extreme circumstances were noted by Berry and Turner (1984, 1986) and Morafka (1994) for the well-studied desert tortoise, *G. agassizii*, and by Adest et al. (1989a) for the Bolson tortoise, *G. flavomarginatus*.

Juvenile desert tortoises are relatively inaccessible in the field for a variety of reasons. The small and inconspicuous animals are often obscured from view by surrounding vegetation, they are sequestered in their burrows up to 98% of the time, and they are active very early in the spring and early in the day (Berry and Turner, 1986; Morafka, pers. obs.). In addition, neonates may disperse rapidly from scattered nest sites, or they may be rapidly depleted by intense predation. Juveniles of many taxa function ecologically as if they were different species from the adults (Polis, 1984). Predator-proof field sites provide opportunities to observe concentrations of juvenile tortoises for sustained periods in a largely natural setting. The resulting insights into the utilization of food, shelter, and water by juveniles are valuable scientifically and contribute to more effective management of critical habitats as well as to the improvement of techniques in population recruitment (Morafka, 1994).

3. Study life history attributes of poorly known species that do not thrive or survive in captivity. Some species of tortoises—e.g., *Homopus boulengeri* (Boycott, 1989; Baard, 1994), *H. femoralis* (Branch, 1989a; Baard, 1994), *Psammobates oculifer* (Boycott and Branch, 1989), *P. tentorius* (Branch, 1989b), and *Pyxis arachnoides* (Durrell et al., 1989a)—do not thrive in captivity. Durrell et al. (1989) noted that there were only five *P. arachnoides* in captivity in 1989, and none had reproduced. The reasons for failure in captivity of these species are unknown. Potential reasons include specialized diets and unusual thermal requirements. For example, Jackson's chameleon, *Chameleo jacksonii*, requires a diurnal temperature of 25 °C and nocturnal temperatures of 10–15 °C (Obst et al., 1988). Similar regimes have been recommended for the central Asian geckos of the genus *Teratoscincus* and many other arid-adapted and upland reptiles.

4. Provide domesticated stock to address human needs: food and pet trade. Occasionally, reptile hatcheries and nurseries are promoted as a means of satisfying local human dietary (and commercial) needs. In addition to the farming of crocodilians, captive-breeding projects for the green turtle, *Chelonia mydas* (Wood, 1982), and the African spurred tortoise, *Geochelone sulcata* (IUCN/SSC, 1989), have been developed to help serve human food needs. However, for tortoises, typically slow-growing compared to homeothermic livestock, these strategies generally prove impractical as they provide a very small and delayed (10–20 years) yield of tortoises (Congdon et al., 1993) in return for a substantial economic investment. No circumstances have been reported in which the production of enclosure- or captive-bred tortoises has significantly reduced the exploitation of wild tortoises for food.

Whether tortoise hatcheries and nurseries could help alleviate the demand for wild juvenile tortoises in the pet trade is a more problematic and controversial issue. Breeding and distribution of tortoises for the pet trade could stimulate demand beyond the capacity of the breeding facilities and thus fuel rather than suppress trade in poached animals. Furthermore, identification of contraband animals is made more difficult for law enforcement, placing a greater burden on inspectors to establish illegal origins. However, leopard geckos (*Eublepharis macularus*), veiled chameleons (*Chameleo calyptratus*), and a few species of boids and colubrids are now bred in such numbers that most of the profit incentive has been removed from smuggling wild-caught conspecifics to American and European markets. In southern California, captive breeding programs have probably alleviated the pressures of collecting on the wild rosy boa, *Lichanura trivergata*. The captive breeding of leopard tortoises, *Geochelone pardalis*, in the United States may be a more germane example (e.g., Street, 1996). Similar breeding programs (in either terraria or field enclosures) established in the exotic pet's country of origin would provide jobs for local communities. The sale of a small percentage of the enclosure-produced neonates could avoid the diminished and delayed financial reward of raising them to adulthood. Such tortoise farms have been advocated to supply the pet trade (e.g., *Testudo h. hermanni*, Kirsche, 1984). Sales of 1–10% of the annual harvest could be considered, especially when alternative funding is not available. However, no recommendation is made here, given the case-specific nature of the risks and benefits in such undertakings.

Recommendations for Future Field Enclosures

1. Develop a plan. Each project should have a well-developed and peer-reviewed plan of action, i.e., established objectives, defined phases, and periods of formal evaluations. Where appropriate, the advice of experts should be sought in the fields of captive breeding, chelonian biology, veterinary medical research and husbandry, and repatriation and reintroduction. The project should be reviewed by appropriate government agencies and community representatives.

2. Utilize the natural setting. The enclosure should include topographical features (with undisturbed substrates) common to the species' natural habitat, appropriate soils for shelter and egg deposition, native vegetation, small native animal species other than tortoise predators, and a sufficient thermal mosaic to allow thermoregulation. Stream channels, washes, and other sites susceptible to temporary flooding should be avoided. Temperature (including sun and shade temperatures at various depths of soil) and precipitation in each enclosure should be monitored frequently to provide data on burrow requirements, activity levels, and thermal preferences. A fully automated, solar-powered weather station can regularly transmit data to computerized logs.

3. Evaluate carrying capacity. One of the more difficult attributes to determine is the carrying capacity of the natural environment or of the enclosure. Data on densities of natural tortoise populations are so limited that scientists are often required to use estimates. Efforts should be made to gather data on densities of wild populations by size class so that appropriate stocking levels for enclosures and for future release programs can be determined. Behaviors of individual tortoises and their intraspecific interactions in the wild should be observed to determine normal patterns, especially territorial tolerances. Such behaviors can then be compared with similar behaviors observed within the enclosures. In the absence of such data, caretakers of the enclosure-maintained animals may miss critical cues of overcrowding.

4. Select genetic stock and maintain genetic diversity. The breeding stock should be carefully selected to maximize heterozygosity and allelic diversity. Because single males or a few dominant males are often responsible for fertilizing most females within a cluster of tortoises (Adest et al., 1984), the risk of inbreeding depression may be higher than total numbers indicate. Even wild North American tortoises have relatively low levels of protein (allozyme) differentiation both within and between species (Morafka et al., 1994). Breeding programs should preserve those regional genetic differences that correlate with adaptive phenotypic differences (MacFarland et al., 1974; Cayot et al., 1994).

Genetic diversity may be enhanced by replacing the breeding stock annually. Small sets of breeding females should not be reused as egg sources because of the potential for genetic bottlenecks and inbreeding depression. Genetic diversity is especially critical for large, highly fecund species such as *Geochelone pardalis*, *G. sulcata*, *G. nigra*, and *Aldabrachelys elephantina* (formerly *Geochelone gigantea*) where a few females could be responsible for large numbers of eggs and their surviving neonates. If the breeding protocol requires an annual turnover of new females as egg sources, this risk is reduced.

If females are locally available, they should be obtained from the wild population adjacent to the enclosure. The locations of their captures should be recorded so that they can be later returned to their home sites. The females should be radiographed, and the gravid females released into the enclosure to deposit eggs. Additional radiographs will confirm whether the eggs have been deposited. Should artificial nest sites and burrows be required, their construction should be undertaken in advance. Females should be returned to their home sites outside the enclosure as soon as possible to avoid overgrazing within the enclosure. If adult scats are to be introduced into the enclosure to benefit potentially coprophagous juveniles, the scats should be taken from clinically healthy animals.

5. Maintain healthy breeding stock, neonates, and juveniles. Health profiles such as blood counts, blood chemistry, and tests for diseases known or suspected to occur in the region should be completed on the proposed breeding stock prior to initiation of the project (Christopher et al., this volume). Once the project is initiated, all animals should be screened annually until released.

Diseases are a growing concern not only in captive but also in wild populations (Jacobson, 1993, 1994). One of the newest and potentially most serious diseases discovered in at least two species of North American tortoises is URTD, caused by the bacterium *Mycoplasma agassizii* (Brown et al., 1994a). The disease is infectious and appears to have been introduced to wild populations through release of captive tortoises (Jacobson, 1993). It is spreading rapidly in wild populations of desert tortoises (Brown et al., 1994b) and is a local problem with the gopher tortoise. In the case of the desert tortoise, some wild populations have suffered catastrophic declines (Berry, this volume). In captivity juvenile tortoises with URTD have been unable to thrive despite careful feeding and nurturing (Oftedal et al., 1995). Adults that survive exposure and illness may have compromised reproductive systems (Lance et al., 1995). All tortoises in hatchery, nursery, and rearing programs should be carefully screened for mycoplasmas (using an ELISA test, Schumacher et al., 1993) as well as other diseases. Protocols should be developed to determine when ill or potentially ill individuals should be removed from experimental programs.

6. Monitor nesting and hatching. Females should be permitted to select nest sites and nest without interference. Frequent (weekly) X-rays (or at least palpation) of adult females should be combined with nest monitoring to determine whether hatching rates are comparable to free-ranging controls. In general, hatching success should be >80% if nests are undisturbed. Stancyk (1982) reported that hatching successes in hatcheries were lower (65%, range = 55–85%) than hatching successes in natural nests (approx. 80%, range = 50–95%) for several species of sea turtles.

Incubation temperatures play a critical role in chelonian hatcheries because sea turtles (Yntema and Mrosovsky, 1980), most freshwater turtle species (Ewert and Nelson, 1991; Pieau and Dorizzi, 1981), and tortoises are subject to temperature dependent sex determination (TSD). Before the role of TSD was known for sea turtles (Yntema, 1976), artificial incubation often produced skewed sex ratios that favored males (Mrosovsky and Yntema, 1980), because eggs were frequently incubated at inadvertently lower temperatures above ground in Styrofoam boxes. Our own enclosure data, previously cited, indicated a similarly skewed sex ratio for *G. agassizii*. The limited data for tortoises, e.g., *Gopherus agassizii* (Spotila et al., 1994) and *Testudo graeca* (Pieau, 1971), suggest that different species have different pivotal temperatures. While higher temperatures favor females in virtually all emydids and testudinids tested, research should be conducted to confirm that TSD affects sex ratios for the species of interest and to determine the pivotal temperature, which in some cases may be population specific (Spotila et al., 1994).

Another important research topic is the range of temperatures suitable for incubation. Incubation temperatures can affect hatching success and later growth of juveniles (Spotila et al., 1994). The fixed-value pivotal temperatures determined by laboratory experiments do not precisely parallel the variable temperatures recorded in nests. While we may expect that a range of suitable temperatures would be present within field enclosures, the enclosed habitat may offer only a small portion of the microenvironments available to free-ranging gravid females. Thus, data should be gathered on daily and seasonal temperature cycles, especially during the time of the sensitive second trimester of incubation (Yntema, 1979; Bull and Vogt, 1981).

7. Provide conditions for development of normal behaviors. Juvenile tortoises should have sufficient space to develop burrows, pallets, and home ranges without abnormal interference from siblings or older or younger tortoises. Naturally occurring vegetation should be sufficient to allow development of normal foraging patterns. Vegetation is also critical for providing an adequately diverse thermal mosaic for thermoregulation. Inadequate cover could expose tortoises to lethal temperatures (e.g., *Gopherus agassizii* and *G. berlandieri* in McGinnis and Voigt, 1971; Rose et al., 1988).

Space should be sufficient to promote normal daily activity and adequate exercise for skeletomuscular development. When tortoises are released from the enclosure, they must be able to navigate, disperse, forage, find or construct shelters, and ultimately locate mates with a capacity comparable to wild-hatched, free-ranging controls.

8. Provide natural diets essential for normal growth, health, and survivorship. Food items must supply an adequate and balanced diet in terms of vitamins, minerals, and especially protein (e.g., 15–17% of total by weight, Adest et al., 1989b). The carrying capacity of the enclosure must be sufficient (i.e., sufficient quantities and distribution of food) to support all the tortoises. In less ideal circumstances, supplemental food, water, and shelter must be provided. Site selection should never be based solely on plant growth and weather data from one season or calendar year. Subsequent years may produce drastic changes in carrying capacity.

General characterizations of ecosystem carrying capacity are likely to be of limited use when tortoises are confined to specific locales. Some tortoise species (e.g., *Gopherus agassizii* and *G. berlandieri*) are characterized as nomadic (Auffenberg, 1969). Some tortoises may qualify as fugitive species (Grimaldi and Jaenicke, 1984), which may simply use ephemeral disclimax or subclimax habitats, and they may shift from site to site to exploit resources. Frail desert grasslands are classic examples as are open habitats created by fire subclimax (Auffenberg, 1969). When normal nomadic movements are curtailed, carrying capacity is likely to be compromised.

Much remains to be learned about the dietary requirements of tortoises in the wild and in captivity (Jackson and Cooper, 1981; Frye, 1991). Numerous crippling and deforming diseases caused by nutritional imbalances and deficiencies have been identified and are likely to occur in tortoises that are raised in hatcheries, nurseries, and other rearing projects. Dietary content should be evaluated and analyses undertaken. Careful records should be kept on environmental conditions, quality and quantity of food items, and amounts of water available. Such data can be used in subsequent evaluations of growth, survivorship, and normal reproductive capacity.

A single adult may need to be present to generate fresh feces bearing the fermenting anaerobic bacterium, *Clostridium bifermentans*, which appears to be instrumental in cellulose digestion for some tortoises (Bjorndal, 1987). Conspecific coprophagy is common in tortoises and iguanas, *I. iguana* (Troyer, 1982; Morafka, 1994), and feces may provide the critical inoculum for the requisite bacteria. The subject of coprophagy requires additional research. Frye (1991) cautions against interspecific coprophagy, but Dezfulian et al. (1994) think consumption of parental feces by neonates may facilitate the inoculation of their large intestines with *Clostridium*, which is assumed to be mutualistic. If scats of adults are made available to the juveniles, the providers of the scats should be clinically healthy.

9. Gather population data for a life table. The demographic attributes (length, mass, sex ratios, density, natality and mortality rates of cohorts, causes of death) of the population should be recorded and analyzed seasonally (preferably) or annually to assess well-being. Annual survivorship records should be kept for each cohort. If survivorship within the enclosure equals or falls below estimates for free-ranging control animals, population and recruitment objectives will not have been met. Data must also be kept on the time required for juveniles to reach reproductive maturity and on the fertility and overall reproductive health of these animals as adults.

10. Conduct a financial analysis and determine cost-effectiveness. Individuals or organizations proposing field enclosure projects should determine how the operations will involve or possibly benefit local human residents. Will jobs for caretakers or monitors be created? Will ecotourism play a role? Are the costs of installation reasonable in light of available financial resources? Is the cost of monitoring and maintenance acceptable? Is the cost for producing each juvenile (and eventually each reproductive adult female) efficient when compared to alternative actions? For each proposed and completed project, a cost analysis should be performed. The cost should be estimated for the production of each emergent neonate, for each juvenile of appropriate size for release, and especially for each juvenile that survives to reproductive maturity.

11. Collect comparable data on wild, free-ranging tortoises. Data on the comparable attributes of free-ranging tortoises are vital to the evaluation of progress within enclosures. Locally-occurring, free-ranging tortoises may serve as valuable controls to their counterparts of the same age classes in the enclosure. Comparisons of the two groups would illustrate differences in growth, health, selection of food and shelter, and most dramatically, in behaviors that may be induced by confinement, higher densities, and artificial protection. Radiotelemetry and emissive tags (pit tags) have greatly increased the practicality of tracking free-ranging tortoises.

Designs for Future Enclosures

Two types of enclosures—permanent pens and mobile, "lift-off" pens—are proposed and varied treatments are reviewed below. The proposed enclosures employ primarily passive management. Female tortoises are temporarily held to deposit eggs, and neonates are raised to conduct life history studies, to restock diminishing wild populations, and/or to repatriate individuals into habitats from which tortoise populations have been extirpated.

Permanent Pens

The permanent pen, such as the design of FISS I at NTC Fort Irwin (Figure 1), offers the cost efficiency of a permanent and reusable structure. Built of durable materials on a stable foundation, it may be less subject to weathering, vandalism, and intrusions, especially by larger carnivores with fossorial proclivities. The permanent structure also lends itself to the installation of automated monitoring systems (such as a solar-powered remote reporting weather station), which are invaluable to the interpretation of life history observations.

The permanent structure also permits the installation of an irrigation system (e.g., sprinklers) for artificially increasing annual precipitation and thereby the available biomass of forage. Such an irrigation system was developed for a small part of the Desert Tortoise Research Natural Area in Kern County, California, for a relocation project encompassing approximately 1.25 km^2 (Science Applications International Corporation, 1993; Mullen and Ross, this volume). Irrigation or sprinkling systems are particularly suitable for desert environments where drought is a common occurrence and where sprinkling during appropriate seasons can enhance the production of food plants used by tortoises. With more forage, juveniles are likely to grow larger at earlier ages (Medica et al., 1975) and have higher rates of survivorship. Also, more juveniles could be maintained in the enclosures.

One previously described concern is the carrying capacity of small enclosures in arid environments. Carrying capacity, often defined as the ability of land to support populations of organisms on a long-term basis, has been determined for very few species and sites. Since carry capacities for juvenile tortoises are unknown for any given study site, densities (expressed as "standing crop" estimates) of juvenile age classes are the best available estimates of natural concentrations of young tortoises. For example, average densities of juvenile and young immature desert tortoises (<140 mm CL, <12 yrs) ranged from 0.43 to 0.75 individuals/ha (0.36–0.98, 95% Confidence Interval) at four long-term study sites in the western Mojave Desert (Berry, 1990; Table 3). These sites were within 50 km of FISS. In contrast, densities of juvenile tortoises at the FISS enclosure ranged from 152 to 305/ha (Table 2), >200× the densities recorded in similar habitats in the wild. If the figures reported for wild settings (Table 3) are used to stock an enclosure, very few individual desert tortoises could be placed in the enclosure without supplemental food and water on a long-term basis.

It is possible that the juveniles may become dependent on receiving adequate food supplies regularly throughout the year, and after release from the enclosure, when irrigation and regular forage are no longer available, they may be subject to rates of mortality higher than that of non-head-started juveniles.

Manipulated Release Program. Some species, such as the desert tortoise, require 5–10 years of growth and shell calcification before they are sufficiently resistant to predators.

Figure 1. The Fort Irwin study site, Enclosure 1, in the central Mojave Desert of California. This enclosure was established to study neonatal and juvenile tortoise biology in *Gopherus agassizii*.

The permanent facility allows the juveniles to achieve the appropriate size-age class—without frequent maintenance or intensive management—before release from the enclosure. At FISS I, when a cohort of juveniles had grown to a size appropriate for release, field workers hand carried them to preformed burrows at random sites 200–300 m from the enclosure. Releases at random sites also avoid local concentrations of prey, which could otherwise concentrate predator attacks or even establish a pattern of subsidized predation. The juveniles were released in the morning to anticipate a 0900–1200 peak of activity.

The principal disadvantage of this strategy is that the increasing concentrations of young tortoises within the enclosure (resulting from holding several cohorts until they are of sufficient size for release) are likely to exceed the carrying capacity. In addition, fixed long-term sites are vulnerable to local weather factors such as wind, flash flood, drought, and fire. Some difficulties may be ameliorated by the construction of up to five subpens to separate each cohort for five years (Morgan and Foreman, 1994). A single subpen is constructed for the first-year cohort, and in subsequent years additional subpens are constructed (one/year) until the first-year cohort reaches the age or size appropriate for release. Then the cycle begins again using the first subpen.

Unimpeded Dispersion Program. Another approach is conceptually similar to the Manipulated Release Program, but juveniles are accorded opportunities for unimpeded, or passive, dispersal from the permanent enclosure. This strategy was implemented by one of us (EKS) in spring 1995 at FISS II, a new enclosure constructed in late fall 1994. A cyclone-fenced enclosure was constructed south of FISS I for this purpose. FISS II has the same general dimensions as FISS I, but is not subdivided into two sections. One- to five-year juvenile tortoises were transferred from FISS I to FISS II and allowed to disperse and establish burrows in April 1995. A few weeks later, ten radio-equipped, 4–5-year tortoises were allowed to establish burrows in the southernmost 20% of FISS II. A barrier was constructed from 20 cm wide flexible, galvanized metal flashing (rising approx. 15 cm above ground, buried to a depth of 5 cm, and held erect by 30 cm metal stakes at approx. 50 cm intervals) to completely isolate the tortoises in the southern one-fifth of the enclosure. While tortoises north of the divider remained confined by the enclosure walls, modifications of the perimeter fencing south of the divider would make it possible for individuals to escape the enclosure entirely. In May, openings 10 cm high × 30 cm wide, flush with the ground, were cut in the fence. The openings converted FISS II into a true exclosure, which now excludes large, non-avian predators but allows juveniles to leave passively. The survivorship rates of passively-released juveniles will be compared with survivorship rates of juveniles released from FISS I.

A possible advantage of this "trickle-out" approach is that a slow, episodic release of individuals may be less likely to provoke interest and attacks by avian and canid predators. The approach also allows juveniles to time their movements to microclimates that are more favorable to their physiologies and to select routes and shelters that provide more protection than those selected by human monitors. Consequently, a more natural dispersion may result, and more natural behaviors may be observed for the released individuals.

The FISS II approach has two potential disadvantages not inherent in other models. First, if predators identify a point of dispersion for juveniles, they may lie in wait or repeatedly return to the site and destroy the stock of dispersing tortoises. A second disadvantage is that tortoises may fail to disperse from the enclosure to the unprotected environment outside.

Mobile Pens

The mobile pen alternative is radically different from the permanent pen: In this modality the enclosure is moved, but not the tortoises within it. In concept, a dome or roofed quadrilateral structure, much like an aviary (but one which excludes birds rather than confines them), could be mounted over a parcel of favorable habitat (good soils, shelters, and forage). The unit should inscribe at least 400 m² (as in a 20 x 20 m square) if it is to provide sufficient carrying capacity for the neonates generated by even a few clutches of eggs. Carrying capacity may be amplified by artificially enhancing precipitation and thereby the food supply. At the Desert Tortoise Research Natural Area, an irrigation system of sprinklers was constructed in a 1.25 km² area. Mobile pens could be placed throughout the area and frequently moved.

Mobile units may also require temporary peripheral foundations of hardware cloth buried 0.3–0.5 m deep and equipped with concrete-anchored posts for mounting the protective fencing. A modular, overhead unit could be assembled from small subunits, which would facilitate both transport to the field and transfer from site to site. The study site would be stocked with tortoises as described above. Given the particularly small size of these units, prompt removal of most females after oviposition would be essential. The time for lifting or moving of the enclosure would be contingent not only on needs of the protected species but also the carrying capacity of the landscape. For example, tortoises may be released during periods when predator populations are low and precipitation and food supplies are high. The modular unit could be relocated to a new site, perhaps with less impacted forage, or to one where natural nesting had already been observed. Tortoises at the previous site would be free to disperse without human intervention, though manipulated dispersion, as described above, could be employed.

This model has the advantages of both low cost and mobility for transfer to other suitable sites. It also can support the tortoises through drought years and may enhance carrying capacity of the site. Such a small enclosure is unlikely to permit normal growth of juveniles. However, as a temporary structure remaining operational for three to six months, this alternative may have fewer negative impacts on the ecosystem and on the behavior of the tortoises that are temporarily confined (especially if they are released within a year of hatching). Temporary structures are more vulnerable to penetration by predators or to destruction by the elements, and the small sizes may lead to overcrowding, depletion of forage, and limited shelter sites.

SUMMARY

For the purposes of this review, we defined predator-proof enclosures as fenced units housing reproducing tortoises and/or their eggs and neonates in natural settings within or peripheral to their historic distributions. Such endeavors were designed to serve two separate functions. First, they concentrated juvenile tortoises in natural but protected settings, making difficult-to-obtain data on life history characteristics accessible. Secondly, enclosures were developed to increase survivorship of eggs, neonates, and juveniles for potential restocking of depleted but contiguous natural populations or for translocation to other sites. Hatcheries, nurseries, and holding facilities also have been developed as tourist attractions and/or public education centers. In developing nations, field-based hatcheries give local residents opportunities to participate in husbandry and release programs that can support, rather than disrupt, local economies and societies. Endeavors addressing these objectives have been operating in North America, the Galápagos Islands, Europe, Africa, Madagascar, and adjacent Indian Ocean islands.

The contributions of enclosures to tortoise biology and conservation, both now and in the future, are more problematic. Certainly these facilities assemble and conserve statistically significant numbers of juveniles in a semi-natural setting. For short-term (single-season) observations, they provide a unique opportunity to study the ecology and behavior of juvenile tortoises when alternatives are prohibitively costly and time consuming. However, scientific accuracy may be compromised. Artificially maintained high-population densities affect behavior, potentially alter socialization, skew sex ratios, and threaten degradation of habitat both from foraging by the tortoises themselves and from foot traffic of human observers working in the pens. These units are most effective when used for the short term, when densities are kept low, and if human intrusion is reduced to a minimum.

The same conditions apply to pens used to enhance recruitment in conservation programs. In the short term, they are an effective technology to reduce nest predation and enhance neonate survival. Juvenile survivorship at fenced sites may be superior to that of equivalent cohorts ranging freely in adjacent field sites. However, we do not know whether these protected sites support growth and behavioral development that result in healthy reproductive adults. Modular enclosures may be relocated to reduce high density impacts on habitat, and permanent units that are equipped with supplemental precipitation systems may improve their carrying capacities and long-term effectiveness. Only when long-term (generational) studies compare tandem cohorts of juveniles raised in pens to their wild counterparts—in terms of survivorship, growth, health, and reproduction—will the success of these enclosures be determined. Our current assessment is that these enclosures are especially useful in filling gaps in tortoise life histories. However, still another decade may pass before we are able to critically judge these experimental projects as conservation tools.

Acknowledgments

The National Training Center at Fort Irwin, California, and Southern California Edison Company supported the research program at the Fort Irwin Study Site, and the World Wildlife Fund provided the grants that supported research at Mapimí. We thank L. Foreman, J. Behler, E. R. Jacobson, and J. Van Abbema for constructive criticisms that substantially improved the manuscript and M. Marolda for editorial assistance. The senior author also thanks S. Williams, Dean of the College of Arts and Sciences, California State University, Dominguez Hills, for providing him with a reduced teaching assignment, which made his participation in this work possible.

Literature Cited

Adest, G. A., G. Aguirre, D. J. Morafka, and J. V. Jarchow. 1989a. Bolson tortoise (*Gopherus flavomarginatus*) conservation: I. Life history. Vida Sylvestre Neotropical 2(1):7–13.

Adest, G. A., G. Aguirre, D. J. Morafka, and J. V. Jarchow. 1989b. Bolson tortoise (*Gopherus flavomarginatus*) conservation: II. Husbandry and reintroduction. Vida Sylvestre Neotropical 2(1): 14–20.

Aguirre, G., G. A. Adest, and D. J. Morafka. 1984. Home range and movement patterns of the Bolson tortoise, *Gopherus flavomarginatus*. Acta Zoológica Mexicana Nueva Serie (1):1–28.

Auffenberg, W. 1969. Tortoise Behavior and Survival. Biological Science Curriculum Study. Patterns of Life Series. Rand McNally Co., Chicago. 38 pp.

Auffenberg, W. and J. B. Iverson. 1979. Demography of terrestrial turtles. *In* M. Harless and H. Morlock (eds.), Turtles: Perspectives and Research, pp. 541–569. John Wiley & Sons, New York.

Baard, E. H. W. 1994. Cape Tortoises. Their Identification and Care. Cape Nature Conservation, Western Cape Province, Cape Town, Republic of South Africa.

Berry, K. H. 1976. A comparison of size classes and sex ratios in four populations of the desert tortoise. *In* K. A. Hashagen (ed.), Proc. Symp. Desert Tortoise Council 1976:38–50. 23–24 March 1976. Desert Tortoise Council, Long Beach, California.

Berry, K. H. 1990. The status of the desert tortoise (*Gopherus agassizii*) in California. Draft report to the U.S. Fish and Wildlife Service, Portland, Oregon.

Berry, K. H. 1997. Demographic consequences of disease in two desert tortoise populations in California, USA. *In* J. Van Abbema (ed.), Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles—An International Conference, pp. 91–99. July 1993, State University of New York, Purchase. New York Turtle and Tortoise Society, New York.

Berry, K. H. and F. B. Turner. 1984. Notes on the behavior and habitat preferences of juvenile desert tortoises (*Gopherus agassizii*) in California. Proc. Desert Tortoise Council Symp. 1984: 111–130.

Berry, K. H. and F. B. Turner. 1986. Spring activities and habits of juvenile desert tortoises in California. Copeia 1986(4):1010–1012.

Bjorndal, K. A. (ed.). 1982. Biology and Conservation of the Sea Turtles. Proceedings of the World Conference on Sea Turtle Conservation, 26–30 November 1979, Washington, D.C. Smithsonian Institution Press, Washington, D.C. 583 pp.

Bjorndal, K. A. 1987. Digestive efficiency in a temperate herbivorous reptile, *Gopherus polyphemus*. Copeia 1987(3):714–720.

Boarman, W. I. 1993. When a native predator becomes a pest: A case study. *In* S. K. Majumdar, E. W. Miller, D. E. Baker, E. K. Brown, J. R. Pratt, and R. F. Schmalz (eds.), Conservation and Resource Management, pp. 190–206. The Pennsylvania Academy of Science, Philadelphia.

Boycott, R. C. 1989. *Homopus boulengeri*: Karoo padloper, Boulenger's padloper, red padloper, biltong tortoise (English); karoo skilpadjie, roosiskilpadjie, donderweerskilpad, biltongskilpad (Afrikaans). *In* I. R. Swingland and M. W. Klemens (eds.), The Conservation Biology of Tortoises, pp. 78–79. Occasional Papers of the IUCN Species Survival Commission (SSC) No. 5. IUCN, Gland, Switzerland.

Boycott, R. C. and W. Branch. 1989. *Psammobates oculifer*: Serrated tortoise, kalahari tent tortoise, kalahari geometric tortoise (English); skulprandiskilpad, kalahari skilpad (Afrikaans). *In* I. R. Swingland and M. W. Klemens (eds.), The Conservation Biology of Tortoises, pp. 88–90. Occasional Papers of the IUCN Species Survival Commission (SSC) No. 5. IUCN, Gland, Switzerland.

Branch, W. 1989a. *Homopus femoralis*: Greater padloper, karoo tortoise (English); vlakskilpad, bergskilpadjie, groter padloper (Afrikaans). *In* I. R. Swingland and M. W. Klemens (eds.), The Conservation Biology of Tortoises, pp. 80–81. Occasional Papers of the IUCN Species Survival Commission (SSC) No. 5. IUCN, Gland, Switzerland.

Branch, W. 1989b. *Psammobates tentorius*. Tent tortoise, starred tortoise, Union Jack tortoise (English); knoppiesdopskilpad, tent-skilpad, sterretjieskilpad, skuwedop, vlakskilpad, vledskilpad (Afrikaans). *In* I. R. Swingland and M. W. Klemens (eds.), The Conservation Biology of Tortoises, pp. 91–93. Occasional Papers of the IUCN Species Survival Commission (SSC) No. 5. IUCN, Gland, Switzerland.

Brown, M. B., I. M. Schumacher, P. A. Klein, K. Harris, T. Correll, and E. R. Jacobson. 1994a. *Mycoplasma agassizii* causes upper respiratory tract disease in the desert tortoise. Infection and Immunity 62(10):4580–4586.

Brown, M. B., P. A. Klein, I. M. Schumacher, and K. H. Berry. 1994b. Health profiles of free-ranging desert tortoises in California: Results of a two-year study of serological testing for antibody to *Mycoplasma agassizii*. Final Report. U. S. Bureau of Land Management, Contract No. B950-C2-0046, Riverside, California.

Buitrago, J. 1981. Percentage of head-started turtles in a population as a criterion. Marine Turtle Newsletter 19:3.

Bull, J. J. and R. C. Vogt. 1981. Temperature sensitive periods of sex determination in emydid turtles. J. Experimental Zool. 218: 435–440.

Carr, A. 1984. Rips, FADS and little loggerheads. BioScience 36: 92–100.

Cayot, L. and G. Morillo. 1997. Rearing and repatriation of Galápagos tortoises: *Geochelone nigra hoodensis*, a case study. *In* J. Van Abbema (ed.), Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles–An International Conference, pp. 178-183. July 1993, State University of New York, Purchase. New York Turtle and Tortoise Society, New York.

Cayot, L. J., H. L. Snell, W. Llerena, and H. M. Snell. 1994. Conservation biology of Galapágos Reptiles: Twenty-five years of successful research and management. *In* J. B. Murphy, K. Adler, and J. T. Collins (eds.), Captive Management and Conservation of Amphibians and Reptiles, pp. 297–305. Contributions to Herpetology, Vol. 11. Society for the Study of Amphibians and Reptiles, Ithaca, New York.

Cheylan, M. 1984. The true status and future of Hermann's tortoise *Testudo hermanni robertmertensi* Wermuth 1952 in western Europe. Amphibia-Reptilia 5:17–26.

Christopher, M., K. A. Nagy, I. Wallis, J. K. Klaassen, and K. H. Berry. 1997. Laboratory health profiles of desert tortoises in the Mojave Desert: A model for health status evaluation of chelonian populations. *In* J. Van Abbema (ed.), Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles—An International Conference, pp. 76–82. July 1993, State University of New York, Purchase. New York Turtle and Tortoise Society, New York.

Congdon, J. L., A. E. Dunham, and R. C. van Loben Sels. 1993. Delayed sexual maturity and demographics of Blanding's turtles (*Emydoidea blandingii*): Implications for conservation and management of long-lived organisms. Conserv. Biol. 7(4):826–833.

Curl, D. A., I. C. Scoones, M. K. Guy., and G. Rakotoarisoa. 1985. The Madagascar tortoise, *Geochelone yniphora*: Current status and distribution. Biol. Conserv. 34:35–54.

Devaux, B. and D. Stubbs. 1997. Species recovery program for Hermann's Tortoise in Southern France. *In* J. Van Abbema (ed.), Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles—An International Conference, pp. 330–332. July 1993, State University of New York, Purchase. New York Turtle and Tortoise Society, New York.

Dezfulian, M., J. Quintana, D. Soleymani, and D. Morafka. 1994. Physiological characteristics of *Clostridium bifermentans* selectively isolated from California desert tortoises. Folia Microbiologia 39(6):496–500.

Diemer, J. 1986. The ecology and management of the gopher tortoise in the southeastern United States. Herpetologica 42(1):125–133.

Dodd, C. K., Jr. 1986. Desert and gopher tortoises: Perspectives on conservation approaches. *In* The Gopher Tortoise and Its Community. Proc. Fifth Ann. Mtg., Gopher Tortoise Council, Florida Museum of Natural History. 93 pp.

Douglass, J. F. 1978. Refugia of juvenile gopher tortoises, *Gopher polyphemus* (Reptilia, Testudines, Testudinidae). J. Herpetology 2:413–415.

Durrell, L., B. Groombridge, S. Tonge, and Q. Bloxam. 1989a. *Acinixys planicauda*: Madagascar flat-tailed tortoise, kapidolo. *In* I. R. Swingland and M. W. Klemens (eds.), The Conservation Biology of Tortoises, pp. 94–95. Occasional Papers of the IUCN Species Survival Commission (SSC) No. 5. IUCN, Gland, Switzerland.

Durrell, L., B. Groombridge, S. Tonge, and Q. Bloxam. 1989b. *Geochelone radiata*: radiated tortoise, sokake. *In* I. R. Swingland and M. W. Klemens (eds.), The Conservation Biology of Tortoises, pp. 96–98. Occasional Papers of the IUCN Species Survival Commission (SSC) No. 5. IUCN, Gland, Switzerland.

Durrell, L., B. Groombridge, S. Tonge, and Q. Bloxam. 1989c. *Geochelone yniphora*: ploughshare tortoise, plowshare tortoise, angulated tortoise, angonoka. *In* I. R. Swingland and M. W. Klemens (eds.), The Conservation Biology of Tortoises, pp. 99–102. Occasional Papers of the IUCN Species Survival Commission (SSC) No. 5. IUCN, Gland, Switzerland.

Ewert, M. A. and C. E. Nelson. 1991. Sex determination in turtle: Diverse patterns and some possible adaptive values. Copeia 1991 (1):50–69.

Frazer, N. B. 1992. Sea turtle conservation and halfway technology. Conserv. Biol. 6(2):179–184.

Frazer, N. B. 1997. Turtle conservation and halfway technology: What is the problem? *In* J. Van Abbema (ed.), Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles—An International Conference, pp. 422–425. July 1993, State University of New York, Purchase. New York Turtle and Tortoise Society, New York.

Frye, F. L. 1991. Biomedical and Surgical Aspects of Captive Reptile Husbandry. Vol. 1, 2nd ed. Kreiger Publishing Co., Malabar, Florida.

Grimaldi, D. and J. Jaenicke. 1984. Competition in natural populations of mycophagous *Drosophila*. Ecology 65:1113–1120.

Hambler, C. 1994. Giant tortoise *Geochelone gigantea* translocation to Curieuse Island (Seychelles): Success or failure? Biol. Conserv. 69:293–299.

IUCN/SSC, Tortoise and Freshwater Turtle Specialist Group. 1989. Tortoises and freshwater turtles: An action plan for their conservation (D. Stubbs, comp.). IUCN/SSC Tortoise and Freshwater Turtle Specialist Group, Gland, Switzerland.

Iverson, J. B. 1982. Adaptations to herbivory in iguanine lizards. *In* G. M. Burghardt and A. S. Rand (eds.), Iguanas of the World, pp. 60–76. Noyes Publishers, Park Ridge, New Jersey.

Jackson, O. F. and J. E. Cooper. 1981. Nutritional diseases, Chapter 12. *In* J. E. Cooper and O. F. Jackson (eds.), Diseases of the Reptilia, Vol. 2, pp. 409–428. Academic Press, Inc. (London) Ltd., London.

Jacobson, E. R. 1993. Implications of infectious diseases for captive propagation and introduction programs of threatened/endangered reptiles. J. Zoo and Wildlife Medicine 24(3):245–255.

Jacobson, E. R. 1994. Causes of mortality and diseases in tortoises: A review. J. Zoo Wildl. Med. 25(1):2–17.

Jacobson, E. R., M. B. Brown, P. A. Klein, I. Schumacher, D. Morafka, and R. A. Yates. 1996. Serologic survey of desert tortoises, *Gopherus agassizii*, in and around the National Training Center, Fort Irwin, California, for exposure to *Mycoplasma agassizii*, the causative agent of upper respiratory tract disease. Abstract. Paper presented at the 21st Annual Meeting and Symposium of the Desert Tortoise Council, 29 March–1 April 1996, Las Vegas, Nevada.

Joyner-Griffith, M. A. 1991. Neonatal desert tortoise (*Gopherus agassizii*) biology: Analyses of morphology, evaporative water loss and natural egg production followed by neonatal emergence in the central Mojave Desert. M.A. thesis, Calif. State Univ., Dominguez Hills, Carson, California.

Kirsche, W. 1984. An F_2-generation of *Testudo hermanni hermanni* Gmelin bred in captivity with remarks on the breeding of Mediterranean Tortoises 1976–1981. Amphibia-Reptilia 5:31–35.

Lance, V. 1995. Sexual diagnosis and differentiation in Fort Irwin desert tortoises, National Training Center, Fort Irwin, California. Contract No. DACA09-93-D-0027, Delivery Order No. 0008, Project 96.8. Robert D. Neihous, Inc., Santa Barbara, California.

Lance, V., D. C. Rostal, J. S. Grumbles, and I. Schumacher. 1995. Effects of upper respiratory tract disease (URTD) on reproductive and steroid hormone levels in male and female desert tortoises. Paper presented at the 20th Ann. Mtg. and Symp. of the Desert Tortoise Council, 31 March–2 April 1995, Las Vegas, Nevada.

Lande, R. and G. Barrowclough. 1987. Effective population size, genetic variation, and their use in population management. *In* M. E. Soule (ed.), Viable Populations for Conservation, pp. 87–123. Cambridge University Press, New York.

Landers, J. L., W. A. McRae, and J. A. Garner. 1982. Growth and maturity of the gopher tortoise *Gopherus polyphemus* in southwestern Georgia, USA. Bull. Florida State Mus. Biol. Sci. 27(2): 81–110.

Legler, J. M. and R. G. Webb. 1961. Remarks on a collection of Bolson tortoise, *Gopherus flavomarginatus*. Herpetologica 17 (1):26–37.

MacFarland, C. G., J. Villa, and B. Toro. 1974. The Galápagos giant tortoise *Geochelone elephantopus* Part 2: Conservation methods. Biol. Conserv. 6(3):198–212.

Martinez, O. E. and J. Morello. 1977. El medio fisico y las unidades fisonomico-floristicas del Bolson de Mapimí. Publicaciones del Insitututo de Ecología, Mexico 3. 63 pp.

Mascort, R. 1997. Land tortoises in Spain: Their status and conservation. *In* J. Van Abbema (ed.), Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles—An International Conference, pp. 307-312. July 1993, State University of New York, Purchase. New York Turtle and Tortoise Society, New York.

McGinnis, S. M. and W. G. Voigt. 1971. Thermoregulation in the desert tortoise, *Gopherus agassizii*. Comp. Biochem. Physiol. 40A:639–643.

Medica, P. A., R. B. Bury, and F. B. Turner. 1975. Growth of the desert tortoise (*Gopherus agassizi*) in Nevada. Copeia 1975(4): 639–643.

Moll, E. O. 1979. Reproductive cycles and adaptations. *In* M. Harless and H. Morlock (eds.), Turtles: Perspectives and Research, pp. 305–332. John Wiley and Sons, New York.

Morafka, D. J. 1977. A biogeographical analysis of the Chihuahuan Desert through its herpetofauna. Dr. W. Junk, B.V., Publishers, The Hague, Netherlands.

Morafka, D. J. 1982. The status and distribution of the Bolson tortoise (*Gopherus flavomarginatus*). *In* R. B. Bury (ed.), North American Tortoises: Conservation and Ecology, pp. 71–94. Wildlife Research Report No. 12, U.S. Dept. of the Interior, U.S. Fish and Wildlife Service, Washington, D.C. 126 pp.

Morafka, D. J. 1993. Juvenile desert tortoise biology. Final 1993 report. Submitted to the Department of Public Works, Natl. Training Center, Ft. Irwin, California. 57 pp.

Morafka, D. J. 1994. Neonates: Missing links in the life histories of North American tortoises. *In* R. B. Bury and D. J. Germano (eds.), Biology of North American Tortoises, pp. 161–173. Fish and Wildlife Research 13, Technical Report Series, U.S. Department of the Interior, National Biological Survey, Washington, D.C.

Morafka, D. J., G. A. Adest, G. Aguirre, and M. Recht. 1981. The ecology of the Bolson tortoise *Gopherus flavomarginatus*. *In* R. Barbault and G. Halfter (eds.), Ecology of the Chihuahuan Desert, pp. 35–78. Instituto de Ecología, A.C., Mexico, D.F.

Morafka, D. J., G. Aguirre L., and R. W. Murphy. 1994. Allozyme differentiation among gopher tortoises (*Gopherus*): Conservation genetics and phylogenetic and taxonomic implications. Canadian J. Zoology 72:1665–1671.

Morafka, D. J., R. A. Yates, J. Jarchow, W. J. Rosskopf, G. A. Adest, and G. Aguirre. 1986. Preliminary results of microbial and physiological monitoring of the Bolson tortoise (*Gopherus flavomarginatus*). *In* Z. Rocek (ed.), Studies in Herpetology, pp. 657–662. 1985, Third Annual Symposium of the Societas Europaea Herpetologica, Prague.

Morgan, L. E. and L. D. Foreman. 1994. Proposal: Hatching and rearing program for desert tortoise. U.S. Bureau of Land Management, California Desert District, Riverside, California. 9 pp.

Mrosovsky, N. 1983. Conserving Sea Turtles. British Herpetological Society, London.

Mrosovsky, N. and C. L. Yntema. 1980. Temperature dependence of sexual differentiation in sea turtles: Implications for conservation practices. Biol. Conserv. 18:271–280.

Mullen, E. B. and P. Ross. 1997. Survival of relocated desert tortoises: Feasibility of relocating tortoises as a successful mitigation tool. *In* J. Van Abbema (ed.), Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles—An International Conference, pp. 140–146. July 1993, State University of New York, Purchase. New York Turtle and Tortoise Society, New York.

Obst, F. J., K. Richter, and U. Jacob. 1988. Completely Illustrated Atlas of Reptiles and Amphibians for the Terrarium. Tropical Fish Hobbyists (TFH) Press, Neptune, New Jersey.

Oftedal, O. T., M. E. Allen, and T. Christopher. 1995. Dietary potassium affects food choice, nitrogen retention and growth of desert tortoises. Paper presented at the 20th Annual Meeting and Symposium of the Desert Tortoise Council, 31 March–2 April 1995, Las Vegas, Nevada.

Pieau, C. 1971. Sur la proportion sexuelle chez les embryons de deux cheloniens (*Testudo graeca* L. et *Emys orbicularis* L.) issus d'oeufs incubes artificielliment. C. R. Hebd. Seanc. Acad. Sci. Paris 272 D:3071–3074.

Pieau, C. and M. Dorizzi. 1981. Determination of temperature sensitive stages for sexual differentiation of the gonads in embryos of the turtle, *Emys orbicularis*. J. of Morphology 170:375–382.

Polis, G. A. 1984. Age structure component of niche width and intraspecific resource partitioning: Can age groups function as ecological species? American Naturalist 123:541–564.

Parmenter, R. R. and H. W. Avery. 1990. The feeding ecology of the slider turtle. *In* J. W. Gibbons (ed.), Life History and Ecology of the Slider Turtle, pp. 257–266. Smithsonian Inst. Press, Washington, D.C.

Pritchard, P. C. H. 1981. Criteria for scientific evaluation of head-starting. Marine Turtle Newsletter 19:3–4.

Rose, F. L., M. E. T. Scioli, and M. P. Moulton. 1988. Thermal preferentia of Berlandieri's tortoise (*Gopherus berlandieri*) and the ornate box turtle (*Terrapene ornata*). Southwest Nat. 33(3): 357–361.

Schumacher, I. M., M. B. Brown, E. R. Jacobson, B. R. Collins, and P. A. Klein. 1993. Detection of antibodies to a pathogenic mycoplasma in desert tortoises (*Gopherus agassizii*) with upper respiratory tract disease. J. Clinical Microbiology 31(6):1454–1460.

Science Applications International Corporation. 1993. American Honda desert tortoise relocation project. Final Report. Science Applications International Corporation, Environmental Programs Division, Santa Barbara, California.

Spotila, J. R., L. C. Zimmerman, C. A. Binckley, J. S. Grumbles, D. C. Rostal, A. List Jr., E. C. Beyer, K. M. Phillips, and S. J. Kemp. 1994. Effects of incubation conditions on sex determination, hatching success, and growth of hatchling desert tortoises, *Gopherus agassizii*. Herp. Mon. 8 (1994):103116.

Stancyk, S. 1982. Non-human predators of sea turtles and their control. *In* K. A. Bjorndal (ed.), Biology and Conservation of the Sea Turtles, pp. 139–152. Proceedings of the World Conference on Sea Turtle Conservation, 26–30 November 1979, Washington, D.C. Smithsonian Institution Press, Washington, D.C. 583 pp.

Stoddart, D. R., D. Cowx, C. Peet, and J. R. Wilson. 1982. Tortoises and tourists in the western Indian Ocean: The Curieuse experiment. Biol. Conserv. 24:67–80.

Street, C. 1996. 1994 hatching-hatchling survey: The results. Tortuga Gazette 32(4):9.

Stubbs, D. 1989a. *Testudo graeca*, spur-thighed tortoise. *In* I. R. Swingland and M. W. Klemens (eds.), The Conservation Biology of Tortoises, pp. 31–33. IUCN/SSC Occasional Papers No. 5., IUCN, Gland, Switzerland.

Stubbs, D. 1989b. *Testudo hermanni*, Hermann's Tortoise. *In* I. R. Swingland and M. W. Klemens (eds.), The Conservation Biology of Tortoises, pp. 34–36. Occasional Papers of the IUCN Species Survival Commission (SSC) No. 5. IUCN, Gland, Switzerland.

Swingland, I. R. 1989. *Geochelone gigantea*, Aldabran Giant Tortoise. *In* I. R. Swingland and M. W. Klemens (eds.), The Conservation Biology of Tortoises, pp. 105–110. Occasional Papers of the IUCN Species Survival Commission (SSC) No. 5. IUCN, Gland, Switzerland.

Swingland, I. R. and M. W. Klemens (eds.). 1989. The Conservation Biology of Tortoises. Occasional Papers of the IUCN Species Survival Commission (SSC) No. 5. IUCN, Gland, Switzerland.

Tom, J. 1994. Microhabitats and use of burrows of Bolson tortoise hatchlings. *In* R. B. Bury and D. J. Germano (eds.), Biology of North American Tortoises, pp. 139–146. Fish and Wildlife Research 13, Technical Report Series, U.S. Department of the Interior, National Biological Survey, Washington, D.C.

Troyer, K. 1982. Transfer of fermentative microbes between generations in a herbivorous lizard. Science 216:540–542.

Turner, F. B., P. Hayden, B. L. Burge, and J. B. Roberson. 1986. Egg production by the desert tortoise (*Gopherus agassizii*) in California. Herpetologica 42:93–104.

Turner, F. B., K. H. Berry, D. C. Randall, and G. C. White. 1987. Population ecology of the desert tortoise at Goffs, California, 1983–1986. Report to Southern California Edison Company, Rosemead, California.

U.S. Fish and Wildlife Service. 1994. Desert Tortoise (Mojave Population) Recovery Plan. U. S. Fish and Wildlife Service, Portland, Oregon. 173 pp. + appendices.

Vasek, F. C. and M. G. Barbour. 1988. Mojave Desert scrub vegetation. *In* M. G. Barbour and J. Major (eds.), Terrestrial Vegetation of California, pp. 835–867. Wiley, New York.

Wood, J. R. 1982. Release of captive-bred green sea turtles by Cayman Turtle Farm Ltd. Marine Turtle Newsletter 20:6–7.

Yntema, C. L. 1976. Effects of incubation temperatures on sexual differentiation in the turtle *Chelydra serpentina*. J. Morphology 150:453–462.

Yntema, C. L. 1979. Temperature levels and period of sex determination during incubation of eggs of *Chelydra serpentina*. J. Morphology 159:17–28.

Yntema, C. L. and N. Mrosovsky. 1980. Sexual differentiation in hatchling loggerheads (*Caretta caretta*) incubated at different controlled temperatures. Herpetologica 36(1):33–36.