Comparative Life Histories of North American Tortoises

by

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Abstract. Since 1978, many studies of the four extant species of North American tortoises (*Gopherus* spp.) were conducted. However, few studies on life-history traits have been made, and data are incomplete or not easily compared across species. The best available data are on gopher tortoises (*G. polyphemus*), but information about the life histories of the Berlandier's tortoise (*G. berlandieri*) and the Bolson tortoise (*G. flavomarginatus*) is incomplete. Only two studies on reproduction of desert tortoises (*G. agassizii*)—both in the Mojave Desert—were published; data about the Sonoran or Sinaloan populations are not available. In North American tortoises, the maximum longevity seems to be 50–70 years; the minimum size at first reproduction for females varies from 140-mm carapace length (CL) in *G. berlandieri* to 285-mm CL in *G. flavomarginatus*; the minimum age at first reproduction varies from 13 years in *G. berlandieri* and *G. agassizii* from the western Mojave Desert to 16–21 years in *G. polyphemus* from the northern part of their range. The mean number of eggs per clutch is 1.4–4.3 in *G. berlandieri* to as many as 8.9 in one population of *G. polyphemus*; the number of clutches per year varies from 0 to 3 (all species); and yearly survivorship of eggs and hatchlings is low but that of adults of all species is high (as high as 100%).

Key words: Age at maturity, clutch frequency, clutch size, *Gopherus*, longevity, reproduction, size at maturity, survivorship.

Four extant species of tortoises (*Gopherus* spp.) occur in North America. All are similar in morphology and phylogeny (Auffenberg 1969; Bramble 1982; Germano 1993; Crumly 1994). They are large reptilian herbivores, and at least two species are important to their communities because their burrows provide shelter for other species (Auffenberg 1969). The North American tortoises differ considerably in length; the smallest (*G. berlandieri*) is about 200 mm in carapace length (CL) and the largest (*G. flavomarginatus*) about 350 mm CL (Morafka 1982; Rose and Judd 1982; Germano 1993). *Gopherus agassizii* and *G. polyphemus* are intermediate in size, and some *G. polyphemus* are slightly larger than some *G. agassizii* (Germano 1989; 1993).

Although all four species of North American tortoises are closely related, two species groups are distinguished by minor skeletal differences and differences in ecology (Auffenberg 1976; Bramble 1982; Crumly 1994). The two largest species, *G. flavomarginatus* and *G. polyphemus*, are more closely related to each other than to either *G. agassizii* or *G. berlandieri* (Auffenberg

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1976; Bramble 1982; Lamb et al. 1989), although *G. agassizii* and *G. berlandieri* are not sister species (Crumly 1994).

Gopherus flavomarginatus and *G. polyphemus* construct long burrows in sandy soils, whereas *G. agassizii* and *G. berlandieri* construct much shallower burrows or, in some parts of both species' range, may not construct burrows (Auffenberg 1969; Germano et al. 1994). The distributions of *G. flavomarginatus* and *G. polyphemus*—but not usually the distributions of populations of *G. agassizii* and *G. berlandieri*—are clumped (Auffenberg 1969; Morafka 1982). Most of the range of *G. polyphemus*, the coastal range of *G. berlandieri*, and the southern part of the range of *G. agassizii* can be considered subtropical (Auffenberg 1969; Germano 1989). In contrast, the entire range of *G. flavomarginatus* is in the Chihuahuan Desert, much of the range of *G. agassizii* is in the Mojave and Sonoran deserts, and the inland portion of the range of *G. berlandieri* is in semiarid scrubland (Auffenberg 1969; Germano 1989).

Sexual dimorphism is greatest in the smallest species, *G. berlandieri*; males have distinct secondary sexual characteristics. The largest species, *G. flavomarginatus*, is least sexually dimorphic. Among the four species, sexual dimorphism inversely correlates with size (Germano 1993). The range of behavioral differences among these species is unknown.

Morphological and ecological differences among *Gopherus* species may significantly affect life history traits. Data on longevity, birth rate, age at first reproduction, survivorship, sex ratio, and age distribution are vital to a complete understanding of these species and to their proper conservation. The Endangered Species Act of 1973 lists all populations of *G. flavomarginatus* as endangered and *G. agassizii* and *G. polyphemus* as threatened in portions of their range. Data on life history traits can be used to simulate population dynamics and to predict the viability of a population. Without these data, little progress in the conservation of these species can be expected.

This paper presents a review of the known life history traits of North American tortoises and includes a comparison of the completeness and accuracy of these data and recommended techniques for further comparisons between species.

Life History Traits

Longevity

Species of *Gopherus* seem to be long-lived, but the actual average and maximum longevities of these species are not known (Table 1). Although some individuals may live 50 to 60 years and possibly longer, many adults may not live that long. No estimates of the maximum age of *G. flavomarginatus* exist. The only estimates of the longevity of *G. berlandieri* are of captive animals and indicate that individuals can live more than 60 years (Judd and McQueen 1982; Judd and Rose 1989). However, longevity is often greater of captive than of wild animals (Gibbons 1987). The estimated longevity of *G. polyphemus* (Landers 1980) is not supported by data on known ages of tortoises in the wild. The estimated longevities of *G. agassizii* (Table 1) are based on tortoises in the wild but are minimum values because of the uncertainty of the accuracy of the estimates (Germano 1992). These estimates also reflect ages of only the oldest individuals, not average longevity. For example, although the oldest adult (≥16 years) *G. agassizii* from the eastern Mojave Desert died when it was about 50 years old, only 17% of the adults lived longer than 25 years (Germano 1992).

The few estimates of the longevity of any chelonians in the wild indicate that *Testudo hermanni* may live about 40 years (Meek 1985), *Geochelone gigantea* 55–70 years (Bourne and Coe 1978), *Che-*

Table 1. Estimated maximum longevity of individuals in the four species of North American tortoises (*Gopherus* spp.).

Species	Age (years)	Source
G. berlandieri	60+[a]	Judd and Rose (1989)
G. agassizii		
Western Mojave Desert	32	Germano (1992)
Eastern Mojave Desert	48–52	Germano (1992)
Sonoran Desert	35	Germano (1992)
Sinaloan habitats	32	Germano (1992)
G. polyphemus	40–60	Landers (1980)
G. flavomarginatus	—	

[a] Captives.

lydra serpentina 60 years (Galbraith and Brooks 1989), *Terrapene carolina* 36–59 years (Schwartz and Schwartz 1991) and 50–80 years (Stickel 1978), and *T. ornata* 32 years (Blair 1976). The estimated longevity of the slider turtle (*Trachemys scripta*) has varied from as many as 75 years (Cagle 1950) to not greater than 30–35 years (Gibbons and Semlitsch 1982; Gibbons 1987). The similarity of the estimated maximum longevity of *Gopherus* species with other chelonians supports the notion that individuals rarely live more than 50–60 years in the wild.

Size at First Reproduction

Data on the size at first reproduction (SFR) of *G. polyphemus* (but not of the other species) are fairly complete (Table 2). Data on male *G. agassizii*, *G. berlandieri*, and *G. flavomarginatus* do not exist. Size at first reproduction of *G. polyphemus* differs in the geographic range of the species and between sexes. The only published data on *G. flavomarginatus* is from a captive female raised in Los Angeles (Morafka 1982), and the relevance of these data to individuals in the wild is unknown. Female *G. berlandieri* first reproduce at 140-mm CL (Judd and Rose 1989), which is the smallest SFR of females in the four species (Table 2).

Techniques for determining SFR may profoundly affect results. The use of radiography is the most effective noninvasive technique for determining the presence of eggs inside a female (Gibbons and Greene 1979) and is becoming widely used. However, the choice of subjects to radiograph in the field may determine or influence the lower limits of size of reproducing females. Until radiography was used in the eastern Mojave Desert, SFR of female *G. agassizii* was considered to be greater than 200-mm CL (Woodbury and Hardy 1948; Burge 1977; Burge and Bradley 1976). However, radiographs of females of less than 200-mm CL showed that some 189–194-mm-CL females reproduced regularly (Turner et al. 1986).

Recent work in the western Mojave Desert revealed smaller SFRs. At a site northeast of Barstow, California, all females and all nonadult tortoises (whose sex could not be determined) were radiographed during spring of 1990, and the second smallest tortoise (176-mm CL) had three eggs (M. A. Griffith, California State University, Carson, personal communication). The sex of *G. agassizii* of less 180-mm CL cannot be determined confidently from shell characteristics. Thus, SFR of *G. agassizii* may be lower than currently reported after smaller individuals will have been examined with radiography.

Techniques for determining SFR of male tortoises have included the examination of secondary sexual characteristics (Landers et al. 1982; Rose and Judd 1982; Diemer and Moore 1994), observation of courtship behavior (Douglass 1976; Landers et al. 1982; Diemer and Moore 1994), and the observation of sperm in seminiferous tubules (Taylor 1982). Data from several sources are available only on *G. polyphemus* and provide the best basis for estimating male SFR (Table 2). Based

Table 2. Minimum size at first reproduction of females and males in the four species of North American tortoises (*Gopherus* spp.).

Species	Carapace length (mm) Females	Carapace length (mm) Males	Source
G. berlandieri	140	—	Judd and Rose (1989)
G. agassizii			
Western Mojave Desert	176	—	M. A. Griffith (unpublished data)
Eastern Mojave Desert	189	—	Turner et al. (1986)
G. polyphemus			
Northern range	250–265	230–240	Landers et al. (1982)
Southern range	226–238	180–230	Auffenberg and Iverson (1979); Iverson (1980); Diemer and Moore (1994); Taylor (1982); Linley (1986)
G. flavomarginatus	285[a]	—	Morafka (1982)

[a] Captive.

only on the appearance of secondary sexual characteristics, male *G. berlandieri* may mature at 110-mm CL (Rose and Judd 1982). Using this criterion, male *G. agassizii* may mature at 180-mm CL (Burge and Bradley 1976), although male characteristics sometimes are evident at 120–140-mm CL (Grant 1936). However, whether the sizes of these three species of *Gopherus* correspond to sexual behavior is not known. Male *G. flavomarginatus* do not have pronounced secondary sexual characteristics (Adest et al. 1989), but sometimes the sex of a male can be confirmed when his carapace length is about 200 mm.

Age at First Reproduction

Based on limited data, female North American tortoises mature at between 13 and 20 years of age (Table 3). Differences in CL do not affect the estimates of age at first reproduction (AFR) because females of the largest (*G. flavomarginatus*) and the smallest (*G. berlandieri*) species mature at approximately the same age. Some females mature when they are only 10 years old (Table 3). The only data on male tortoises pertain to *G. polyphemus* and indicate that males reach maturity at a slightly younger age than females (Table 3).

The most complete data on AFR are of *G. polyphemus*. Data on the other species are based on one study (Germano 1994). In all cases, the age of an individual is determined by counting growth annuli on either the carapace or the plastron. The age at which most females first started to reproduce is usually estimated from a regression of age to SFR (Germano 1994; Diemer and Moore 1994). Therefore, the accuracy of AFR depends on knowing the size at which females first produce eggs. This makes the estimated AFRs of *G. flavomarginatus* and the Sonoran and Sinaloan populations of *G. agassizii* equivocal. The estimated age of *G. flavomarginatus* is based on a single captive individual, and the estimated ages of the Sonoran and Sinaloan populations of *G. agassizii* are based on size to maturity of tortoises from the eastern Mojave. Whether this size is accurate for the Sonoran and Sinaloan populations is not known. Comparable data on AFR will be possible only when SFRs of *G. flavomarginatus* , *G. agassizii*, and *G. berlandieri* are reliably estimated.

Number of Eggs per Clutch

The information about the number of eggs per clutch in *G. flavomarginatus*, *G. agassizii*, and *G. berlandieri* is incomplete (Table 4). On clutch size, ten studies of wild *G. polyphemus*, three studies of wild *G. berlandieri*, two studies of wild *G. agassizii* (one from the eastern Mojave Desert

Table 3. Minimum age at first reproduction (range) of females and males in the four species of North American tortoises (*Gopherus* spp.).

Species	Age (years) Females	Males	Source
G. berlandieri	13.3(11–17)		Germano (1994)
G. agassizii			
Western Mojave Desert	13.0(9–18)		Germano (1994)
Eastern Mojave Desert	15.4(12–19)		Germano (1994)
Sonoran Desert	15.7(11–21)[a]		Germano (1994)
Sinaloan habitats	13.8(12–15)[a]		Germano (1994)
G. polyphemus			
Northern range	16–21	16–18	Landers et al. (1982); Germano (1994)
Southern range	13.6(10–16)	ca. 10	Iverson (1980); Linley (1986); Germano (1994); Diemer and Moore (1994)
G. flavomarginatus	13.9(12–17)[b]		Germano (1994)

[a] Ages based on minimum size-at-first reproduction of eastern Mojave Desert *G. agassizii*.
[b] Captive.

and one from the western Mojave Desert), one study of captive *G. agassizii* (not counting anecdotal reports), and one study of captive *G. flavomarginatus* (Table 4) are available. The largest clutch size is of *G. polyphemus* from the southern part of its range, and the smallest is of *G. berlandieri*. Clutch sizes in the Sonoran and Sinaloan populations of *G. agassizii* and in wild populations of *G. flavomarginatus* have not been published.

Number of Clutches per Year

The number of clutches per year ranges from 0 to 3, and means by species and region range from 1.0 to 1.7 (Table 4). Techniques to determine the number of clutches per year have included examining dead specimens (Auffenberg and Weaver 1969; Iverson 1980; Rose and Judd 1982), using oxytocin to induce egg deposition (Adest et al. 1989), measuring sudden weight changes (Turner et al. 1984), and applying periodic radiography (Turner et al. 1986; Judd and Rose 1989; Diemer and Moore 1994).

Three studies of *G. polyphemus* revealed that females lay 1 clutch/year (Table 4). Earlier, it was believed that *G. berlandieri* deposited as many as 2 or more clutches/year (Auffenberg and Weaver 1969; Rose and Judd 1982). It has been suggested that females lay only one clutch annually (Judd and Rose 1989). No supporting data were given for the estimated average of 1.39 clutches/female by wild *G. flavomarginatus* (Adest et al. 1989), but this estimate indicates that some females lay more than 1 clutch/year. Captive female *G. flavomarginatus* can have as many as 3 clutches/year (Table 4). The fecundity of *G. agassizii* in its range in the western Mojave, Sonoran, or Sinaloan deserts is not known, but two studies in the eastern Mojave Desert revealed common multiple clutching (Turner et al. 1986, 1987). Both studies were based on frequent measurements, and one study (female tortoises radiographed every 10 days) indicated that most females had 2 clutches/year and one female had 3 clutches in 2 of 3 years (Turner et al. 1986).

Double and triple clutching in North American tortoises seem to be limited to *G. agassizii* from the eastern Mojave Desert and perhaps to *G. flavomarginatus* but may be more widespread. One

Table 4. Mean number of eggs per clutch (range, number of clutches) and mean number of clutches per year (range) in the four species of North American tortoises (*Gopherus* spp.).

Species	Mean: Eggs per clutch	Mean: Clutches per year	Source
G. berlandieri	1.42(1–3,73)	ca. 2	Auffenberg and Weaver (1969)
	4.30(3–7,10)	1–2	Rose and Judd (1982)
	2.65(1–5,29)	1	Judd and Rose (1989)
G. agassizii	6.71(2–14,7)[a]	1–2[a]	Miller (1955)
Western Mojave Desert	(1–7,39)	—	M. A. Griffith (unpublished data)
Eastern Mojave Desert	4.50(1–8,107)	1.73(0–3)	Turner et al. (1986)
		1.60(0–2)	Turner et al. (1984)
G. polyphemus			
Northern range	7.0(4–12,47)	1	Landers et al. (1980)
	3.5(1–6,4)	—	Marshall (1987)
	5.3(1–7,7)	—	Marshall (1987)
Southern range	5.2(1–9,32)	1	Iverson (1980)
	6.7(2–10,24)	1	Taylor (1982); Diemer and Moore (1994)
	7.8(5–10,16)	—	Linley (1986)
	7.6(3–25,32)	—	Godley (1989)
	8.9(5–11,11)	—	Burke (1987)
	5.8(3–10,62)	—	Diemer and Moore (1994)
G. flavomarginatus	6.0(3–9,9)[a]	ca. 2(0–3)[a]	Morafka (1982)
		1.39	Adest et al. (1989)

[a] Captive.

study of the reproduction of *G. polyphemus* was based on dissections of museum specimens and recently killed tortoises (Iverson 1980), and the investigator stated that *G. polyphemus* laid only 1 clutch/year. However, the data are of the duration of the reproductive cycle and not of the number of the deposited clutches. Graphic data (Fig. 1 *in* Iverson 1980) showed enlarged follicles or eggs in females from late March until late June, whereas tabular information indicated the presence of enlarged follicles from October to May and oviductal eggs from April to June. The latter interval is perhaps long enough for the production of more than 1 clutch/year.

Female *G. polyphemus* in the northern portion of their range reportedly lay 1 clutch/year based on periodic examinations of burrow mouths and surrounding areas for signs of nesting (Landers et al. 1980). However, how frequently burrows were examined and whether nesting immediately after an inspection could be detected during a subsequent visit are unclear. Finally, whether any females failed to reproduce in a given year was also not known (Landers et al. 1980). One study with radiography to detect clutches of eggs in female *G. polyphemus* revealed that only one clutch was deposited annually, but females were usually radiographed only once a year (Diemer and Moore 1994).

Similarly, data on *G. berlandieri* suggest only one clutch of eggs annually, but radiographs were taken every 2 weeks and the investigators pointed out that multiple clutches could have been missed in some cases (Judd and Rose 1989). This study further revealed that egg production begins in April, but radiographs were not taken at 2-week intervals until 20 May.

Consistent multiple clutches in wild populations of North American tortoises were found only in *G. agassizii* from the eastern Mojave desert (Turner et al. 1984, 1986), where tortoises were evaluated at intervals shorter than 2-weeks. Female tortoises were radiographed every 10 days between late April and early to mid-July (Turner et al. 1986). The short intervals between radiographing may have been the reason for the discovery of multiple clutches. Until these studies, no data indicated that wild *G. agassizii* laid more than 1 clutch/year. Although female *G. polyphemus* and *G. berlandieri* may only lay 1 clutch/year, the data are equivocal.

Survivorship

From Egg to Emergence From the Nest

Survivorship of any age class of *G. berlandieri* (Judd and Rose 1989) or of *G. agassizii* from Sonoran or Sinaloan habitats have not been estimated (Table 5). The only estimated clutch survivorship in *G. berlandieri* is an estimate of egg fertility.

Clutch survivorship in *G. agassizii* in the eastern Mojave Desert, which was estimated from nest destruction, was 24–28% in 1983 (Turner et al. 1987) and 70% in 1984 (Roberson et al. 1989; F. B. Turner and K. H. Berry, unpublished report to Southern California Edison Company, 85-RD-63). The estimated fertility was 88%, but the estimated hatching rate was only 46% in nests protected from predation. This low hatching rate may have been due to the effects of human disturbance when eggs were moved.

In contrast, the hatching rate in tortoises from a western Mojave Desert study site was high (Table 5). In this study (M. A. Griffith, California State University, Carson, personal communication), gravid females were placed in a large enclosure in native habitat close to where they were captured. The females deposited eggs in nest sites they constructed, and the eggs were incubated in an undisturbed nest free from predation. I used this fertility rate with the estimates of nest destruction to estimate clutch survivorship in tortoises from the eastern Mojave Desert (Table 5).

In southwestern Georgia, 34 of 38 nests of *G. polyphemus* were destroyed (11% survivorship), although 154 of 179 protected eggs hatched at an 88% fertility rate (Table 5). The estimated clutch survivorship of *G. flavomarginatus* (Adest et al. 1989) is not supported by data and may not be accurate.

The survivorship of clutches should be interpreted with caution. Predation seems to be a major cause of clutch failure, but exact estimates of clutch survival are not easily produced. Tinkle et al. (1981) pointed out that, when Cagle (1950) reported counting 500 destroyed nests of *Chrysemys picta* and only one intact nest, this could not be interpreted as only 1 surviving clutch of 500 clutches because the actual total number of nests in the area was unknown. Investigators may find nests that have been disturbed by predators more easily than intact nests.

From Hatching to Year One

The survival rate (51%) of *G. agassizii* hatchlings (Table 5) was estimated from smaller-than-80-mm-CL tortoises (F. B. Turner and K. H. Berry, unpublished report to Southern California Edison Company, 85-RD-63), which probably included 2–3-year-old individuals. The low survivorship of *G. polyphemus* (Table 5) is the estimated survivorship from egg to age 1, which integrates two sets of survivorship estimates. Furthermore, this low estimate is based solely on counts of burrows and may partially represent a failure to locate small burrows. The estimated survivorship of *G. flavomarginatus* (Table 5) was based on a group of 11 hatchlings that was followed for 1 year. Five died in 11 months (54.5% survivorship), only three were found a year later (27.2% survivorship), and the fates of another three individuals were not known (Tom 1988).

From Year One to Maturity

The yearly survivorship of *G. agassizii* (Table 5) was estimated by the skeletal remains on two plots in the eastern Mojave Desert and was 71% of ≤180-mm CL tortoises during 1977–80 and 89% of 81- to 160-mm CL tortoises during 1983–84 (F. B. Turner and K. H. Berry, unpublished report to Southern California Edison Company, 85-RD-63). I used the sizes of these tortoises to estimate the survivorship to maturity, but these estimates only roughly correspond to correct ages. Furthermore, these estimates are only crude approximations and may not accurately reflect survivorship (F. B. Turner, University of California, Los Angeles, personal communication); I included them because they are the only available estimates.

Similarly, the estimated survivorship to maturity of *G. polyphemus* (Table 5) is only approximate. One estimate was made with a Jolly–Seber model and pertains to less than 100-mm CL and 100–199 mm CL tortoises (J. E. Diemer, unpublished report to Florida Game and Fresh Water Fish Commission, Study 7536). Many assumptions

Table 5. Estimates of survivorship in the four species of North American tortoises (*Gopherus* spp.) at four life stages.

Species	Eggs laid to hatching (%)	Hatching to year one (%)	Year one to maturity (%)	Adult (%)
G. berlandieri	60[a,b]	—	—	—
G. agassizii				
Western Mojave Desert	93[a,c]	—	—	83.7–100[d]
Eastern Mojave Desert	46–67[e]	51[e]	71–89[g,e]	75–98[e]
G. polyphemus				
Northern range	11–86[a,f]	—	—	—
Southern range	—	5.8[h]	53–66[g,j]	44–95[j]
			12.5–79[i]	—
G. flavomarginatus	12.5–65[a,k]	27.2–54.5[l]	60–96[k]	—

[a] Fertility.
[b] Rose and Judd (1982).
[c] M. A. Griffith (personal communication).
[d] Berry (1986).
[e] Turner and Berry (unpublished report).
[f] Landers et al. (1980).
[g] Tortoises 1–4 years old followed for 1 year.
[h] Alford (1980).
[i] Diemer (unpublished report).
[j] Wilson (1991).
[k] Adest et al.(1989).
[l] Tom (1988).

for this model were not met. The other estimated survivorship is of 1–4-year-old tortoises that were followed for 1 year (Wilson 1991). Of 32 tortoises that were fitted with radio transmitters, 11 were dead and 4 were missing after 1 year (Wilson 1991).

The survivorship of *G. flavomarginatus* (Table 5) was estimated from 27 tortoises marked as juveniles (117–198-mm CL) between 1980 and 1985 (Adest et al. 1989). Only 2 of these tortoises were later found alive in the colony—5 dead were found, and the disposition of the remaining 20 was unknown (Adest et al. 1989). If the remaining 20 tortoises were alive but not found, the mean yearly survivorship of this group was about 96%; if only the 2 tortoises found in the colony after 5 years survived, the yearly rate was about 60%.

Adults

The only estimated adult survivorship was of *G. agassizii* from the Mojave Desert and of one population of *G. polyphemus* (Table 5). This may have been due in part to the ease of finding skeletal remains of tortoises in the Mojave Desert, from which death rates of adults are computed. Vegetation in most other parts of the range of the North American tortoises is considerably more dense and may impede finding remains. Although the habitat is fairly open, few adult *G. flavomarginatus* are ever found (Bury et al. 1986). Alternatively, adult *G. flavomarginatus* may die in their burrows, which may be as long as 10 m.

The estimated adult survivorship of *G. agassizii* from the Californian portion of its range is high (Berry 1986). These estimates were obtained during 3–9 year studies at 14 sites and indicate that mortality was low in the eastern Mojave Desert and moderate to high in the western Mojave Desert (Berry 1986; Corn 1994). The usual survivorship of adult *G. agassizii* seems to be high, but occasionally adult mortality is high in some years (Turner et al. 1987; Germano and Joyner 1989).

The population dynamics of tortoises in North America are not well known (Auffenberg and Iverson 1979). Survivorship of different age classes and their interrelations will be difficult to determine but must be determined for an understanding of the responses of North American tortoises to their environment and to perturbations.

Conclusion and Recommendations

More data on the life histories of North American tortoises are needed. The fecundity, longevity, and survivorship of all species—especially of Sonoran and Sinaloan populations of *G. agassizii* and inland and Mexican populations of *G. berlandieri*—have to be determined. Studies of fecundity should be patterned after the study of *G. agassizii* in the eastern Mojave Desert (Turner et al. 1986). At least 30 reproductive female tortoises should be studied and fitted with radio transmitters, so that they can more easily be found during the breeding season. Each female should be X-rayed every 10 days from the onset to the end of the breeding season. Radiographing should continue until the investigator is certain no more eggs are being produced. However, the possibility of detrimental effects on females or eggs from periodic exposure to X-rays should be evaluated first.

In addition to studies of clutch size in adult tortoises, the smallest size at which females and males can reproduce should be determined. Radiography should be used for the detection of eggs in larger-than-90-mm-CL *G. berlandieri*, in larger-than-150-mm-CL *G. agassizii* and *G. polyphemus*, and in larger-than-200-mm-CL *G. flavomarginatus* to determine the lower limits of female reproductive maturity. Injections of the cloacae with water should be used for the detection of sperm in known males and in smaller individuals whose sex is not ascertained and in which eggs are not found. The same males should be monitored to determine the age at which males begin to exhibit sexual behavior.

The ages of all individuals must be determined. The age of many tortoises can be determined by the counting of scute rings by a technician who has learned to distinguish annuli from false rings (Germano 1988; Germano and Joyner 1989). A thin section of scute of older tortoises can be taken for later age determination or, at least, the individual can be assigned an age group (e.g., >25 years old). Counts of growth rings of North American tortoises as old as 20–25 years are reasonably accurate (Landers et al. 1982; Germano 1988, 1992). Easily seen scute rings in individuals that are older than 25 years are no longer useful, but sections of thin scute may be used to determine the age of older individuals (Germano 1992). Other nondestructive techniques of aging living tortoises have yet to be developed. Counts of scute rings should be made in a random sample of tortoises that are studied in the field.

Data on small individuals are important missing information of the demography of tortoises. Locating small tortoises can be aided by using dogs, which have been successful in finding box turtles (Schwartz et al. 1984). Dogs have shown some promise for locating desert tortoises in California (K. H. Berry, Bureau of Land Management, Riverside, California, personal communication) and Arizona (personal observation), but there has been no consistent testing. Recent work with radio-tagging hatchling tortoises and following them for extended periods will help determine survivorship rates, but many studies and large sample sizes will be needed to accurately determine rates and patterns of hatchling and juvenile survivorship.

Determination of survivorship is perhaps most difficult but efforts should continue because tortoises lend themselves to long-term studies of demography. With recent advances of aging tortoises, the age of any young and subadult individual can be determined. This allows the building of static life tables. Combining the ability to age individuals with effective mark–recapture–study areas will provide information about the survivorship of the age groups.

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Bolson tortoise (*Gopherus flavomarginatus*), Mapimi Field Station, Mexico, 1988. *Photo by D. J. Germano.*