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Home Range and Movements of North American Tortoises

Home range and movements of North American tortoises are influenced in both dramatic and subtle ways by climatic factors, topographical features, burrowing substrate, forage availability, social interactions, anthropogenic disturbances, and the physical structure of vegetation. Home range has been defined by Burt (1943) as “that area traversed by the individual in its normal activities of food gathering, mating, and caring for young.” A number of methods used in determining “home range” exist, and the merits of each have been discussed elsewhere (Calhoun and Casby 1958, Jennrich and Turner 1969, Anderson 1982). Descriptions of habitat characteristics for each species are covered in chapter 9, and details of basking, overwintering, social interactions, and egg-deposition sites are discussed in chapters 4, 12, and 13. Although we overlap with some of those topics, our objectives are to explain why, when, and how far tortoises move. Here, we discuss all North American tortoises (genus *Gopherus*), following nomenclature of Crother (2008) for *G. polyphemus*, *G. flavomarginatus*, and *G. berlandieri*. We use the recent division of the desert tortoise (Murphy et al. 2011) into *G. agassizii* and *G. morafkai*.

HOME RANGE SIZE AND DISTANCES MOVED

Although generalities do exist regarding movements of North American tortoises, considerable individual and site-related variation has been observed in home range size and distances moved for *Gopherus polyphemus* (McRae et al. 1981, Diemer 1992a, Wilson et al. 1994, Butler et al. 1995, RB Smith et al. 1997, Mitchell 2005), *G. berlandieri* (Auffenberg and Weaver 1969, Rose and Judd 1975, Judd and Rose 1983, Kazmaier et al. 2002), *G. flavomarginatus* (Aguirre et al. 1984), and both species of desert tortoise (Burge 1977, Hohman and Ohmart 1980, Turner et al. 1980, Medica et al. 1981, Barrett 1990, Martin 1995, Duda et al. 1999, Averill-Murray et al. 2002a, Franks et al. 2011, Nussear, unpublished data). Judd and Rose (1983)

summed it up by noting: “Perhaps the single most striking aspect of the home range ecology of *G. berlandieri* is the great variability among individuals in home range size.” This behavioral plasticity and intersite variation are both intriguing and confounding, especially when trying to estimate minimum area requirements for preserves (Eubanks et al. 2002, Mitchell 2005).

In general, both species of desert tortoise make longer movements and have larger home ranges than the other three species of North American tortoises; however, Kazmaier et al. (2002) documented relatively large home ranges for the diminutive *G. berlandieri*. Overlapping home ranges tend to be the norm for North American tortoises (McRae et al. 1981, Aguirre et al. 1984, Diemer 1992a, O’Conner et al. 1994b, Averill-Murray et al. 2002a, Kazmaier et al. 2002). On average, adult males of all five species tend to travel more frequently, move longer distances, and have larger home ranges than adult females (McRae et al. 1981, Aguirre et al. 1984, Diemer 1992a, O’Conner et al. 1994b, RB Smith et al. 1997, Averill-Murray et al. 2002, Kazmaier et al. 2002, Eubanks et al. 2003, Franks et al. 2011). This difference between sexes is not surprising, considering the intensive mate-seeking that males undertake (McRae et al. 1981, Douglass 1986, Diemer 1992a, Averill-Murray et al. 2002a, Kazmaier et al. 2002, Boglioli et al. 2003, Eubanks et al. 2003). An exception to the above trend has been documented at two sites in southern Nevada (Bird Spring Valley and Lake Mead), where adult female *G. agassizii* had home ranges nearly double that of males (Nussear, unpublished data). Furthermore, some immature tortoises have larger home ranges than some adults (Aguirre et al. 1984, Diemer 1992a, Butler et al. 1995, Kazmaier et al. 2002, Pike 2006).

Taking into account variations in habitat type, climatic factors, study duration, sample size, and data analysis, mean home ranges (minimum convex polygons) for adult and immature North American tortoises are shown in table 11.1. In some cases, tortoises moved only between two burrows

Table 11.1. Home range sizes (minimum convex polygons) of North American (*Gopherus*) tortoises

Species	Number by sex / size class	Mean Home Range (ha)	Minimum/Maximum Home Range (ha)	Duration of Study (yr)	State/Habitat type	Reference
<i>G. polyphemus</i>	8 M	0.45	0.06–1.44	<1	GA sandhill	McRae et al. 1981
	5 F	0.08	0.04–0.14	<1	GA sandhill	McRae et al. 1981
	68 M	1.10	0.00–4.80	1	GA longleaf pine	Eubanks et al. 2003
	51 F	0.40	0.00–3.40	1	GA longleaf pine	Eubanks et al. 2003
	43 F	1.86	0.01–13.49	2	GA sandhill	Mitchell 2005
	7 M	1.05	0.28–2.17	<1	FL W. Indian scrub	McLaughlin 1990
	6 F	0.06	0.01–0.12	<1	FL W. Indian scrub	McLaughlin 1990
	6 M	0.88	0.23–2.88	1–2	FL planted pine	Diemer 1992b
	5 F	0.31	0.00–1.18	1–2	FL planted pine	Diemer 1992b
	8 F	0.48	0.00–1.44	1	FL sandhill	Smith 1995
	6 F	0.11	0.00–0.48	1	FL old field	Smith 1995
	10 M	1.90	0.30–5.30	1–2	FL coastal scrub	Smith et al. 1997
	4 F	0.60	0.30–1.10	1–2	FL coastal scrub	Smith et al. 1997
	9 M	0.32	0.13–0.63	<1	FL beach dunes	Lau 2011
	11 F	0.42	0.01–2.94	<1	FL beach dunes	Lau 2011
	11 M	1.95	0.63–4.89	1–2	MS burned pine	Yager et al. 2007
	9 F	1.07	0.11–2.46	1–2	MS burned pine	Yager et al. 2007
	9 M	1.30	0.71–2.43	1–2	MS unburned pine	Yager et al. 2007
	11 F	1.90	0.21–7.65	1–2	MS unburned pine	Yager et al. 2007
	4 S	0.50	0.01–0.25	1–2	FL planted pine	Diemer 1992b
7 J	0.01	0.00–0.25	1–2	FL planted pine	Diemer 1992b	
9 J	0.07	0.01–0.36	1	FL sandhill	Wilson et al. 1994	
9 H	0.25	0.06–0.42	1–2	FL sandhill	Butler et al. 1995	
7 H	1.95	0.01–4.81	1	FL coastal scrub	Pike 2006	
<i>G. flavomarginatus</i>	5 M	5.35	—	1–2	MX desert grassland	Aguirre et al. 1984
	6 F	4.72	—	1–2	MX desert grassland	Aguirre et al. 1984
	9 J	1.10	—	1–2	MX desert grassland	Aguirre et al. 1984
	5 J	22.3 m ²	—	1	MX desert grassland	Tom 1988
	4 J	28.4 m ²	—	1	MX desert grassland	Tom 1988
	— M	3.1	—	—	MX desert grassland	Adest 1994
	— F	2.5	—	—	MX desert grassland	Adest 1994
	— J	0.4	—	—	MX desert grassland	Adest 1994
<i>G. berlandieri</i>	31 M	2.57	—	2–5	TX salt flats, lomas	Judd and Rose 1983
	26 F	1.42	—	2–5	TX salt flats, lomas	Judd and Rose 1983
	9 F	6.8	1.5–21.6	2	TX mesquite/catclaw, ungrazed	Kazmaier et al. 2002
	7 M	31.8	9.2–130.7	2	TX mesquite/catclaw, ungrazed	Kazmaier et al. 2002
	13 F	5.0	1.0–19.8	2	TX mesquite/catclaw, grazed	Kazmaier et al. 2002
	7 M	9.5	4.8–23.2	2	TX mesquite/catclaw, grazed	Kazmaier et al. 2002
<i>G. agassizii</i>	— M	53	39–77	—	CA creosote/bursage	Berry 1974
	— F	21	8–46	—	CA creosote/bursage	Berry 1974
	3 M	26	20–38	1.5	NV creosote/bursage	Burge 1977
	3 F	19	11–27	1.5	NV creosote/bursage	Burge 1977
	5 M	23	2–34	2	AZ creosote/bursage	Hohman and Ohmart 1980
	3 F	11	1–29	2	AZ creosote/bursage	Hohman and Ohmart 1980
	2 S	3.5	3.4–3.5	2	AZ creosote/bursage	Hohman and Ohmart 1980
	4 M	1.3	0.22–3.4	1	AZ creosote/ bursage/blackbrush	Esque 1994
	6 F	3.5	1.2–11.0	1	AZ creosote/ bursage/blackbrush	Esque 1994
	10 F	5.6	0.3–11.85	1	UT creosote/ bursage/blackbrush	Esque 1994
	10 F	10.3	0.11–14.6	2	UT creosote/ bursage/blackbrush	Esque 1994
	1 M	4.41	—	1	UT creosote/ bursage/blackbrush	DeFalco 1995
	4 F	3.65	3.0–4.5	1	UT creosote/ bursage/blackbrush	DeFalco 1995
	17 M	26.6	2.9–88.6	1	CA creosote/bursage	Turner et al. 1980
	38 F	19.0	2.9–88.6	1	CA creosote/bursage	Turner et al. 1980
	25 M	24.5	1.6–72.7	1	CA creosote/bursage	Medica et al. 1981
	52 F	23.7	1.6–2.7	1	CA creosote/bursage	Medica et al. 1981
	13 M	7.65	3.8–16.9	1	CA creosote/bursage	Duda & Krzysik 1998
16 F	7.49	1.0–15.9	1	CA creosote/bursage	Duda and Krzysik 1998	

(continued)

Table 11.1. (cont.)

Species	Number by sex / size class	Mean Home Range (ha)	Minimum/Maximum Home Range (ha)	Duration of Study (yr)	State/Habitat type	Reference
	14 M	3.11	0.0–14.4	1	CA creosote/bursage	Duda and Krzysik 1998
	15 F	0.91	0.01–3.7	1	CA creosote/bursage	Duda and Krzysik 1998
	34 F	22.24	2.22–109.7	4	NV creosote/bursage	Nussear unpub. data
	22 M	11.95	1.70–33.83	4	NV creosote/bursage	Nussear unpub. data
	5 S	32.92	5.79–102.45	2–3	NV creosote/bursage	Nussear unpub. data
	7 F	24.45	1.97–124.35	2	NV creosote/bursage	Nussear unpub. data
	9 M	14.27	1.09–38.61	2	NV creosote/bursage	Nussear unpub. data
	7–16 F	5.3–7.2	—	1–2	CA creosote	Franks et al. 2011
	5 M	16.2	—	<1	CA creosote	Franks et al. 2011
	18–22 F	7.6–9.1	—	1–2	CA creosote	Franks et al. 2011
	6 F	1.6	—	<1	CA creosote	Franks et al. 2011
	5 M	9.2	—	<1	CA creosote	Franks et al. 2011
	4 F	2.1	—	<1	CA creosote	Franks et al. 2011
	4 M	5.8	—	<1	CA creosote	Franks et al. 2011
	8 M	20.9	7.7–40.0	<1	NV creosote/bursage	O'Connor et al. 1994b
	7 F	9.0	5.9–13.6	<1	NV creosote/bursage	O'Connor et al. 1994b
<i>G. morafkai</i>						
	9 M	9.2	1.0–22.3	2	AZ Arizona upland	Averill-Murray et al. 2002a
	4 F	4.7	2.7–7.5	2	AZ Arizona upland	Averill-Murray et al. 2002a
	4 M	21.7	15.2–31.5	2	AZ interior chaparral	Averill-Murray et al. 2002a
	6 F	23.3	3.4–51.5	2	AZ interior chaparral	Averill-Murray et al. 2002a
	10 F	12.8	2.3–50.7	2	AZ Arizona upland	Averill-Murray et al. 2002a
	5 M	25.8	5.6–53.4	1.5	AZ palo verde / cacti mixed shrub	Barrett 1990
	9 F	15.3	2.8–48.5	1.5	AZ palo verde / cacti mixed shrub	Barrett 1990
	4 M	11.0	3.9–22.2	2	AZ desert grassland	Averill-Murray et al. 2002a
	4 F	2.6	1.1–6.0	2	AZ desert grassland	Averill-Murray et al. 2002a
	3 M	16.3	3.3–25.2	2	AZ semidesert grassland	Martin 1995
	3 F	13.1	8.1–21.6	2	AZ semidesert grassland	Martin 1995

Note: For the number by sex / size class column, M = males, F = females, J = juveniles, S = subadults, and H = hatchlings.

during the study period, and their home ranges could not be computed. Home ranges may be overestimated by minimum convex polygons, which can include significant areas that tortoises may not use; however, this analysis has been widely employed, and its pros and cons have been discussed in the literature (O'Connor et al. 1994a, Kazmaier et al. 2002, Pike 2006, Harless et al. 2010). Home ranges derived using this method are perhaps best considered as indicators and estimators of movement scales and patterns (O'Connor et al. 1994a) and may be most useful in interpreting home ranges for habitat conservation purposes (Pike 2006, Harless et al. 2010).

Some researchers studying *G. polyphemus* have divided movements into those associated with feeding and those related to social interactions (McRae et al. 1981, Smith 1995). Mean feeding radius from the burrow in a southwest Georgia sandhill was 13 m, with 95% of feeding activity occurring within 30 m of the burrow (McRae et al. 1981). In north Florida sandhills, Smith (1995) reported that female *G. polyphemus* foraged within 17 m of their burrow, and Ashton and Ashton (2008) described a similar radius as the primary forage area around the burrow and 100 m as a secondary forage radius that is less frequently used. Auffenberg and Iverson (1979) cited the connection between foraging distance and food availability/quality, and noted that food is so plentiful in much

of the range of *G. polyphemus* that most individuals usually move < 50 m from their burrows to feed. *G. polyphemus* also undertakes longer movements (e.g., 1–3+ km), however, apparently associated with seasonal depletion of preferred forage or highly selective foraging (McRae et al. 1981, Ashton and Ashton 2008). In some habitats, *G. polyphemus* commonly feeds along grassy roadsides and uses roadways and fire lanes as travel corridors during social encounters, thereby elongating home ranges (McRae et al. 1981, Douglass 1990, Diemer 1992a, RB Smith et al. 1997).

In contrast to *G. polyphemus*, *G. flavomarginatus* does not appear to increase movements in response to decreases in quantity and diversity of forage; instead, the tendency for *G. flavomarginatus* is to decrease the distance of movements during seasons of less forage abundance and increase them during the season of major productivity (Aguirre et al. 1984). For *G. agassizii*, home ranges in the same habitat may vary from one year to the next with changing environmental factors, such as rainfall. The overall mean home range of *G. agassizii* in Ivanpah Valley, California, varied from 19.0 ha for females and 26.6 ha for males in 1980, a year of high ephemeral plant production (7.3–10.0 g/m²) (Turner et al. 1980), to 16.5 ha for females and 23.0 ha for males in 1981 (a drought year with ephemeral production of 0.04–0.11 g/m²) (Medica et al. 1981). Similarly,

G. agassizii home ranges at both the Sand Hill and Pinto Basin sites at Twentynine Palms, California, were much larger in 1995, a productive year for winter annuals, than the drought year of 1996 (Duda and Krzysik 1998, Duda et al. 1999).

Movements of hatching *G. polyphemus* have been studied on several sites in Florida and Mississippi. Mean distance from the nest to the first burrow is generally ≤ 15 m (Butler et al. 1995, Epperson and Heise 2003, Pike 2006). Dispersal from the nest is random, and hatchlings move farther from the nest over time (Pike 2006). Mean daily movements are relatively short, averaging 8 m (Butler et al. 1995, Epperson and Heise 2003, Pike 2006), but some individuals make longer movements (e.g., 80 m in a 24-hour period; Epperson and Heise 2003). Mean daily movements for older juveniles are similar (McRae et al. 1981, Diemer 1992a, Wilson et al. 1994), with some longer forays. *Gopherus flavomarginatus* juveniles exhibit relatively high motility and also expand their activity area as they become larger in body size (Aguirre et al. 1984).

Comparing movements within and among tortoise species is complicated by how tracking data are collected. In general, daily maximum movements of *G. polyphemus* within home ranges (e.g., 200–400 m; Diemer 1992a, Smith 1995) are shorter than those of *G. flavomarginatus* (>900 m; Aguirre et al. 1984) and other western species. Emigrating *G. polyphemus*, however, have been known to move 0.7–6.4 km over periods ranging from about four days to more than three months (Diemer 1992a, Eubanks et al. 2003). *Gopherus agassizii* commonly travel 470–823 m/day (Berry 1974), and males are known to cover >1000 m/day within their home range. Some individuals have traveled longer point-to-point distances (1.4–7.3 km) outside their usual activity area over periods ranging from 16 days to five years (Berry 1986a); similarly, Kazmaier et al. (2002) documented an 11-km dispersal by a juvenile *G. berlandieri* over one year. One of the longest movements was by a radio-telemetered female *G. morafkai* that traveled 32 km from the Rincon Mountains south to the Santa Rita Mountains in Arizona. This tortoise's journey over anthropogenic barriers (railroad tracks and interstate highways) was facilitated by researchers and it was even temporarily adopted and held in captivity by private citizens on several occasions (Edwards et al. 2004a). *Gopherus morafkai* historically dispersed between mountain ranges and despite the challenges posed by anthropogenic habitat modifications, such as interpopulation movements may be critical to the persistence of small tortoise populations (Edwards et al. 2004a).

Erratic behavior and movements prior to long-distance dispersal have been reported for both *G. polyphemus* (Diemer 1992a) and *G. flavomarginatus* (Aguirre et al. 1984). Diemer (1992a) noted that a subadult *G. polyphemus*, which eventually emigrated 0.7 km from its natal colony over about four days, moved back and forth along a forestry windrow for several days before its dispersal, even crawling up onto the debris and precariously balancing on logs. Dispersing immature and adult *G. flavomarginatus* exhibited erratic movements within relatively small areas (0.2–0.7 ha) before making extended, almost straight, advances (1–6 km), generally in a single direc-

tion. These individuals were not transients at the time of their displacement and had been members of their colonies for at least two years before making their long-distance dispersal (Aguirre et al. 1984).

Gopherus polyphemus movements and home ranges are also influenced by natural vegetation succession, forestry practices, and land management practices, such as controlled burning (Landers and Speake 1980; Auffenberg and Franz 1982; Diemer 1986, 1992a). *Gopherus polyphemus* in thickly planted pines or in areas that do not receive controlled burns may move to roadsides or natural openings in the forest (Landers and Buckner 1981, Diemer 1992a). Anthropogenic disturbance also can prompt movements to different burrows or excavation of new burrows, and may provide tortoises with alternative burrowing terrain such as berms and windrows (Diemer 1992a). Although disturbance can prompt movement by *G. polyphemus*, it does not necessarily result in significant changes in home range (Mendonca et al. 2007, Yager et al. 2007). In contrast to the response of *G. polyphemus* to disturbance, Kazmaier et al. (2002) reported significantly larger home ranges for *G. berlandieri* in ungrazed pastures than in grazed pastures, but noted that research design and analysis method could have affected this finding.

DAILY ACTIVITY AND SEASONALITY OF MOVEMENTS

Gopherus polyphemus is almost exclusively diurnal, although rare nocturnal activity by both adults and juveniles occur (Alexy et al. 2003; Ashton and Ashton 2008; T. Radzio, personal communication). Ashton and Ashton (2008) observed individuals foraging as late as midnight in northern Florida during July to September when daytime temperatures exceeded 36°C . Both *G. polyphemus* (T. Radzio, personal communication) and *G. flavomarginatus* (Adest et al. 1988) are known to emerge during nocturnal rain events. Nocturnal emergence by *G. flavomarginatus*, with or without rainfall, may be related to elevated burrow or soil temperatures and may occur more widely than was once thought (Adest et al. 1988). Nocturnal activity in *G. agassizii* has been observed at Lake Mead National Recreation Area in southern Nevada (elevation ~ 500 m), where temperatures in summer reach $\sim 49^{\circ}\text{C}$ in the daytime and commonly are still greater than 38°C at sunrise (Nussear 2004). At a higher elevation (~ 1020 m) at Rock Valley, Nevada, a large male *G. agassizii* was observed in its burrow at dusk before a nocturnal thunderstorm; it exited the burrow during the night and was observed at sunrise under a shrub surrounded by a fresh moat of dry mud (P. Medica, personal observation). Modern technology (e.g., remote video cameras) can provide 24-hour coverage of burrows (Alexy et al. 2003; T. Radzio, personal communication), improving future understanding of tortoises' responses to diel and climatic factors.

Daily activity by *G. polyphemus* generally is unimodal, with a midday peak, and follows the daily temperature cycle (Douglass and Layne 1978, McRae et al. 1981, Alexy et al.

2003), especially during the spring months. In southern Florida, the activity peak was during the hottest hours, 1300–1600, throughout the year (Douglass and Layne 1978). McRae et al. (1981) noted a bimodal activity pattern during July and August in southwest Georgia, however, with feeding forays more common during 1000 to 1200 and 1600 to 1800; activity returned to a unimodal pattern following the intense summer heat. A bimodal activity pattern in July–August occurs in *G. flavomarginatus* (Morafka et al. 1981). *Gopherus berlandieri* on the coast had two diel activity periods in spring, with a primary peak during 1000 to 1100 and a secondary peak during 1700 to 1800 (Bury and Smith 1986). Seasonal variation in the daily activity of *G. agassizii* is observed, with the pattern unimodal in spring and fall, but bimodal during the warmer summer months (Woodbury and Hardy 1948, Luckenbach 1982, Zimmerman et al. 1994).

Seasonal activity of *G. polyphemus* varies latitudinally, depending on the severity of winter temperatures. In much of its range, *G. polyphemus* is most active May–August and least active December–February (Douglass and Layne 1978, McRae et al. 1981, Diemer 1992a). In south-central Florida, some activity occurs outside the burrow every month of the year (Douglass and Layne 1978). On the southeast Florida coast, *G. polyphemus* engages in courtship year-round; there is no winter dormancy, although activity may wane during late January into early February (Moore et al. 2009). Morafka (1982) reported that winter dormancy of *G. flavomarginatus* generally extends from November through April. Activity of both species of desert tortoise also varies greatly with latitude and elevation. Activity extends into early December on Tiburon Island, Sinaloa, Mexico (Bury et al. 1978). The onset of hibernation for *G. agassizii* at four sites in Nevada and Utah during winter 1998–1999 was from 15 October to 10 November and was dependent upon the cooler fall temperatures at the study site (Nussear et al. 2007). In an extensive four-year study at Yucca Mountain, Nevada, involving 365 individuals, most entered hibernation during October or the first half of November, with 98% entering hibernation by 15 November with some variation based upon size and sex (Rautenstrauch et al. 1998). Eighteen percent of the juvenile *G. agassizii* at Fort Irwin, California were active above ground on winter days when temperatures were above 10°C (Wilson et al. 1999a).

Nesting tends to dictate late spring movements of adult female *G. polyphemus*, and relatively long-distance movements can occur as females search for open-canopied, sunlit egg-deposition sites during May and June (Landers 1980, McRae et al. 1981, Diemer 1992a, Smith 1995). Female *G. berlandieri* also made long-distance forays up to 0.8 km during May–June (Kazmaier et al. 2002). Similarly, Averill-Murray et al. (2002a) observed a female *G. morafkai* moving 0.75 km from its usual home range in June presumably to lay eggs. An extended movement of 1.3 km took place for a nesting female *G. agassizii* in Ivanpah Valley, California, between June 1980 and March 1981 (Medica et al. 1981).

Increased late summer and early fall movements by male *G. polyphemus* are well documented in both Georgia and

Florida (McRae et al. 1981, Douglass 1990, Diemer 1992a, Eubanks et al. 2003) and coincide with the period of active spermatogenesis (Taylor 1982a, Ott et al. 2000). The outermost points of the home range of a male *G. polyphemus* may represent the burrows of preferred females; thus, female locations are important in determining the limits of males' home ranges (Douglass 1990; J. Diemer, personal observation). Male *G. berlandieri* and *G. morafkai* also make relatively long forays during late summer (Averill-Murray et al. 2002a, Kazmaier et al. 2002), although a long movement (3.1 km) by a male *G. agassizii* was observed in Ivanpah Valley, California, during 14–30 May 1980 (Turner et al. 1980).

Juvenile *G. polyphemus* (one–four years old) in west-central Florida were active during every month of the year (Wilson et al. 1994), with activity peaking in spring. Winter movements were limited, but juveniles basked more often on the burrow mound in winter than in other seasons. On the east-central Florida coast, Pike (2006) documented year-round activity in hatchling *G. polyphemus*, but noted that they moved the most during and immediately following the time of hatching (August–November). Butler et al. (1995) found consistently high activity of hatchling *G. polyphemus* from mid-April through early November in northeast Florida; activity then waned until late March.

BURROW/SHELTER-SITE USE

Unlike *Gopherus berlandieri* and the two species of desert tortoise, *G. polyphemus* and *G. flavomarginatus* almost universally excavate relatively deep burrows for shelter (Hansen 1963, Auffenberg 1969, Morafka et al. 1981, Morafka 1982). Ashton and Ashton (2008) recorded their longest *G. polyphemus* burrow as 20.5 m. Exceptions to the typically deep burrows are found in areas with lime rock or high water tables, or in shell-sands of the coast and off-shore islands; in these situations, burrows may be quite shallow (Auffenberg 1969, Ashton and Ashton 2008). Both adult and juvenile *G. polyphemus* occasionally use shallow depressions known as pallets (Auffenberg 1969, Diemer 1992a, Butler et al. 1995, Ashton and Ashton 2008), but not nearly as frequently as do the primarily non-burrowing *G. berlandieri* (Rose and Judd 1982). Both species of desert tortoise use a variety of burrows, dens, pallets, and other shelter-sites (Luckenbach 1982). In the northern extreme of the geographic range on the Nevada Test Site, *G. agassizii* burrows can extend 7.5 m under caliche overhangs in the sides of washes (Germano et al. 1994). Some tortoises in Nevada also shelter under shrubs overnight during July–September (Bulova 1994). *Gopherus morafkai* excavates soil burrows but also uses caliche caves in washes, rock crevices, vegetation, and even nests of wood rats (*Neotoma albigula*) as shelter-sites (Martin 1995, Averill-Murray et al. 2002a).

Individual and site-related variations are also reflected in number of burrows used by *G. polyphemus*. Depending on season, this species uses multiple burrows (McRae et al. 1981, Diemer 1992a, RB Smith et al. 1997, Eubanks et al. 2003). In longleaf pine (*Pinus palustris*) habitat in Georgia, females used

an average of five burrows and males used ten burrows in one year (Eubanks et al. 2003), similar to earlier findings (females: four; males: seven; McRae et al. 1981) in comparable habitat for a slightly shorter period (April–December). In a Florida pine plantation, mean number of burrows used was three for females and six for males (April–December); males averaged eight burrows over two years (Diemer 1992a). Mean number of burrows used over one to two years was larger in a Florida coastal scrub habitat: nine for females and 17 for males (RB Smith et al. 1997). Eubanks et al. (2003) noted that most studies were not long enough to fully elucidate the number of burrows that a particular *G. polyphemus* uses during its lifetime; previously unoccupied burrows are continually being added to an individual's roster. Like *G. polyphemus*, male *G. flavomarginatus* also use a greater number of burrows ($n = 4$), on average, than females ($n = 3$) (Aguirre et al. 1984). Although male *G. agassizii* may use an average of 17.6 shelter-sites in a year and females may use 19, the majority of those used by males are burrows rather than nonburrows (Burge 1977). On another Nevada study area, *G. agassizii* used an average of 9.1 shelter-sites (range, 3–18) during July to October (Bulova 1994). *Gopherus morafkai* in southern Arizona may use as many as 27 shelter-sites (average, 21) over a two-year period (Martin 1995).

Hatchlings and other juvenile *G. polyphemus* may use pallets, abandoned adult burrows, or shelter under vegetation (Diemer 1992a, Butler et al. 1995, Ashton and Ashton 2001, Pike 2006); they also dig new burrows as they disperse from the nest area (Butler et al. 1995, Pike 2006). Depending on the site and tracking duration, this youngest class of *G. polyphemus* may use an average of one to five burrows (Wilson et al. 1994, Butler et al. 1995, Epperson and Heise 2003, Pike 2006). Hatchlings and older juvenile *G. flavomarginatus* use an average of two burrows (Aguirre et al. 1984), and like *G. polyphemus*, they shelter in pallets and under vegetation (Tom 1994).

Although burrows generally contain only one *G. polyphemus* at a time, co-occupation during the day or even overnight has been documented for both adults and immatures (McRae et al. 1981, Douglass 1990, Diemer 1992a, Pike 2006). Burrow or other shelter-site co-occupation has also been observed in

other species of *Gopherus* (Rose and Judd 1982, Aguirre et al. 1984, Averill-Murray et al. 2002a). Cohabitation of burrows by both males and females is infrequently observed among *G. agassizii*; particularly during late summer and early fall, males have been frequently observed within burrows with females at Rock Valley, Nevada (P. Medica, personal observation). Burrow defense or usurpation may be associated with these social encounters; individuals of *G. polyphemus* will turn sideways within burrows and block the forward motion of tortoises trying to enter (Diemer 1992a). Similarly, individuals of *G. flavomarginatus* and *G. morafkai* defend their burrows against intruders (Aguirre et al. 1984, Averill-Murray et al. 2002a), and female *G. morafkai* have even been observed defending their burrows containing nests against Gila monsters (*Heloderma suspectum*) (Barrett and Humphrey 1986). Because *G. berlandieri* does not excavate deep burrows, individuals generally use pallets on a "first-come, first-served" basis and do not defend these depressions; moreover, these pallets do not serve as the central focus of *G. berlandieri* activity, as do the burrows of the other *Gopherus* species (Rose and Judd 1982).

CONCLUSIONS

The home range and movements of North American tortoises are strongly influenced by both environmental and anthropogenic factors, and therefore vary considerably among species, geographic locations, and individuals. In general, male *Gopherus* tortoises have larger home ranges than females, with a few exceptions documented for *G. agassizii*. Movements are closely tied to foraging needs and social interactions, but there are unknown factors that influence relatively long-distance dispersals. Although primarily diurnal, *Gopherus* species do occasionally engage in nocturnal activity. Two of the five species, *G. polyphemus* and *G. flavomarginatus*, generally excavate relatively deep burrows; the other three species use a variety of created or existing shelter-sites that include burrows, pallets, dens, and caves under rocks or caliche. Despite intensive research efforts over the last four decades, these tortoise species remain, in some ways, enigmatic.

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